ABSTRACT This article covers the origin and development of scientific interest in insect and amphibian developmental biology at the Department of Systematic Zoology and Zoogeography of the Jagiellonian University. The greater part of this historical account is devoted to Professor Stanislaw Smreczynski (1899-1975), the founding father of the Department, and comments on his biography and research achievements in the field of animal experimental embryology. A particular emphasis is on Smreczynski’s contributions to contemporary understanding of early embryonic development of amphibians and insects as well as his expertise in Pleistocene and extant weevils (Curculionidae). A concise survey of developmental phenomena studied by some of Smreczynski’s co-workers and followers is also presented, including the early embryogenesis of entognathans as well as germ cell determination and gonad formation in Drosophila virilis conducted by Jura; analysis of oogenesis in Collembola carried out by Krzysztofowicz; investigations of insects and tardigrades by Weglarska, and finally research into various aspects of ovary structure in diverse insect taxa by the Bilinski group.

KEY WORDS: history, developmental biology, insect, amphibian experimental embryology, oogenesis
was promoted full professor in 1956. After the doctorate, he expanded his zoological training first in Lwow working with L. Hirshler, and then in Berlin and Paris, where he collaborated with R. Heymons and C. Pérez, respectively.

When Smreczynski began a 23-year career as a head of the Department, it constituted of 6 more scientists and 4 technicians. They had at their disposal a lecture room, a demonstration room, a small library and several rooms cluttered with old furniture, an extensive collection of microscope samples, jars filled with formalin-fixed specimens and pieces of mostly obsolete scientific equipment (Fig. 2). A shining star of the equipment was a Reichert light microscope with phase contrast, a gift of the Rockefeller Foundation.

The early post-war years were highly unfavorable for the development of science in Poland due to enormous devastation of the country and a dramatic loss of the professional academic staff. Later, during the first decades under the communist rule in Poland, travel and communication with the West were severely restricted, so scientists coped not only with a profound lack of funds for the advancement of science but more importantly almost non existing access to current scientific ideas and literature, which gradually led to severe isolation. In such non-enticing scientific environment Smreczynski did his research with tremendous passion and enthusiasm and was a constant source of stimulation and encouragement for his colleagues.

In 1951 Smreczynski was elected a dean of the Faculty of Mathematics and Nature and was instrumental in creating an independent unit, the Faculty of Biology and Earth Sciences. In 1963, when the Institute of Zoology was founded, Smreczynski became its first director and remained in office till 1968. He retired in 1969 but continued to work on weevil taxonomy until his death on April 6th 1975. It is worth adding here that Smreczynski was a long time editor of the *Acta Biologica Cracoviensia, series Zoology* and an assistant editor of the *Folia Biologica*. He was a member of the Polish Academy of Arts and Sciences and fellow of the Polish Entomological Society, the Polish Zoological Society, the International Union of Biological Sciences - section Entomology, and the Société Entomologique de France.

There are two clearly separated periods in Smreczynski’s scientific activity. Before the World War II he spent most of his time studying early stages of amphibian and insect embryonic development. It is amazing how broad was the scope of his research interest and the ease he switched between various developmental systems to explore their particular value in explaining specific
developmental phenomena. Inspired by Spemann’s experiments on newts and salamanders, and encouraged by his mentor Godlewski, Smreczynski embarked with great enthusiasm on several projects concerning various aspects of amphibian development. One of these projects addressed a much debated and at the time controversial issue of the localization of the cytoplasmic material from which the neural plate develops in the frog embryos. He conducted numerous experiments in which he inflicted slight physical damage to various regions of the early cleaving embryos using fine glass needles. These experiments led him to conclusion that in frogs the material from which the neural plate develops resides within the cytoplasm of the animal hemisphere of the egg (Smreczynski, 1927). He also studied the sensitivity of the eggs and early embryos to mechanical injury and found that there was an anterior-posterior gradient of the ability to compensate for the damage. At that time, the glass needles, hair loops and binocular microscopes were the primary research tools of embryologists, and the analysis could not proceed beyond the cellular level. Later, inspired by the Spemann’s research, Smreczynski analyzed regulatory mechanisms during frog development as well as the significance of the dorsal lip region for the gastrulation process (Smreczynski, 1929).

Professor Smreczynski found also the insect world endlessly fascinating and devoted several years of his life investigating the development of these creatures. In particular, he studied the formation of body segments during embryogenesis and became actively involved in the heated debate over the number of segments in the insect head. Because a continuous layer of cuticle covers the insect head, it is impossible to tell from its external morphology alone how many segments it contains. At the beginning of XX century entomologists profoundly disagreed over the exact number of segments in insect head and different groups opted for 5, 6 or even 7 segments. Smreczynski’s reports (1931, 1932) on the embryonic development of the head in a burying beetle, Silpha obscura contributed to the currently held view that there are six segments. The controversy over the head segments was, as it may seem, an artificially created academic problem, but one with far-reaching implications for the evolution of different arthropod groups and their phylogenetic links. These issues ignite a considerable interest of scientists to the present day. The evidence coming from earlier, purely descriptive morphological research is now extended and corroborated by the studies of genes responsible for the patterning of the body, including Hox genes, which specify the identity of insect segments (Averof and Akam, 1995). Other Smreczynski’s valuable contributions to insect embryology are: a detailed description of the embryonic envelope formation in the weevil Phyllobius glaucus (Smreczynski, 1934) and a comprehensive account of the embryonic development of the beetle Agelastica alni (Smreczynski, 1938). These studies made lasting contributions to entomology textbooks. Smreczynski’s work in insect embryology has been a powerful stimulus to others and his ideas will continue to influence and illuminate many aspects of the field.

Smreczynski’s adventure with embryology came to an abrupt end with the outbreak of the World War II. After the war, with his deteriorating sight and increasing burden of administrative duties, Smreczynski devoted himself entirely to taxonomy of Coleoptera, in particular weevils (Curculionidae) and became a world-famous expert on both Pleistocene and extant curculionids. Throughout the years he created an extensive collection of beetles, now housed at the Department of Systematic Zoology and Zoogeography. His vital contribution to coleopteran taxonomy has been recognized in several eponyms, e.g. Smicronyx smreczynskii; S. solari 1952; Rhynchaeus smreczynskii; Dieckmann 1958; Otiorhynchus smreczynskii; Cmoluch 1968; Apion smreczynskii, Bajtenov 1979.

Professor Smreczynski was renowned for his immense erudition and considered a thinker of great originality. His exceptionally good memory made him a reliable source of various nature facts. He was not only comprehensively educated zoologists but also a man of considerable personal charm so he easily attracted people to work with him. As a leader, he created a friendly atmosphere and skillfully stimulated interest in scientific problems in his students. He always showed considerable tact and patience with students, but at the same time he was a demanding examiner and zoology exams ranked high on the student list of difficulty. Some of his detailed exam questions concerning insect anatomy became legendary.

Smreczynski was able to convey his enthusiasm for embryological experiments and passion for investigating insects as well as other animals to a group of his students, among them Zofia Bielanska-Osuchowska, Anna Czapik, Czeslaw Jura, Zbigniew Kawecki, Anna Krzysztofowicz, Wiktor Micherdzinski, Boguslaw Petryszak, Barbara Wegiarska and others (Fig. 3). Due to space limitation, selected research results of only a few Smreczynski’s students are briefly presented.

In 1960s researchers in the Department were predominantly concentrated on the precise description of morphological changes during insect embryonic development. More modern experimental and histochemical approach became possible with acquiring technically more advanced pieces of equipment like Zeiss light microscopes, ultramicrotomes and Tesla transmission electron microscopes. Thanks to scholarships the communication with foreign academic centers became more vivid enabling exchange of ideas and contacts with up-to-date scientific information and equipment.

Inspired by Smreczynski, his former students Jura and Krzysztofowicz became interested in various aspects of develop-
ental biology of Entognatha, a group of relatively small, wingless and otherwise inconspicuous arthropods, considered to be a sister group to true insects (*Insecta s. str.*; Hennig, 1981; Kristensen, 1981). Entognatha, comprising Protura, Collembola and Diplura, remain poorly studied yet they are extremely interesting for developmental biologists and zoologists alike. They are the most primitive group within Hexapoda and may provide valuable clues about the evolution of certain features within the entire arthropod group. For instance, in most insects, egg undergoes an unusual type of development called syncytial (superficial) cleavage, which initially encompasses only nuclear divisions. The formation of membranes separating the superficially located nuclei, i.e. cytokinesis, occurs much later in development. It is not entirely clear how this type of cleavage evolved and in this respect the entognathans are of particular interest because this arthropod group contains a wide spectrum of transitions from total to truly superficial cleavage.

The studies initiated by Jura and continued together with Krzysztofowicz and collaborators focused on development of a representative of Collembola, *Tetrodontophora bielanensis*. This springtail lays spherical eggs, covered by a vitelline envelope and chorion. The eggs are rich in yolk, centrolecithal but in contrast to the eggs of most insects, do not contain the yolk-free periplasm. During fertilization 2-4 sperms enter the oocyte (Jura and Krzysztofowicz, 1992). Surprisingly, as Jura demonstrated in sectioned material, the early cleavage of fertilized eggs is initially total, i.e. nuclear divisions are followed by cytokinesis, and continues until the embryo reaches the eight-blastomere stage (Fig. 4A; Jura, 1965). Subsequently, a superficial cleavage is initiated and a rather complex sequence of divisions forms a periblastula (Fig. 4B, C) (reviewed in Jura, 1972). Jura addressed also a puzzling problem of gastrulation in collembolan embryos as well as the differentiation of the blastoderm into the germ band, dorsal organ and embryonic membranes (Jura 1965, 1967b). He also investigated the midgut formation and the origin of endoderm, probably the most controversial and disputed issues in entognathan embryology. He proposed, that the midgut primordium forms during embryonic development from the blastomeres, which initially contribute to yolk and turn into vitellophages (Jura, 1966).

Careful and methodical studies of entognathan reproduction and development focused at some point on the structure of the ovary in Protura and especially Collembola, almost completely unknown at the time. Investigating the processes of germ cluster formation, yolk accumulation and egg envelope deposition Jura and collaborators found some similarities with *Insecta s. str.*., but more importantly, some essential differences as well. The ovaries of Collembola and Protura are sac shaped and not divided into a discrete ovarioles as in majority of insects (Jura, 1975; Krzysztofowicz, 1977). The ovaries in Protura are of the peculiar, neopanoistic type, while those in Collembola are polytrophic-meroistic (reviewed in Bilinski, 1994). Later works by Bilinski and Klag showed, contrary to a traditional view, that the entognathan oocytes are indeed covered by somatic cells resembling a simple follicular epithelium (Bilinski, 1977, 1979; Klag, 1978). Moreover, there are gap junctions present between the oocyte and the surrounding somatic cells and, as in other insect systems, they are likely to coordinate differentiation of the connected cells (Bilinski and Klag, 1982). Although the formation of germ cell clusters in collembolan ovaries has not been entirely elucidated, it was demonstrated that the germline clones are not branched as in most meroistic insect ovaries but linear (reviewed in Bilinski, 1994). It was also found that in Collembola and some Diplura the oocyte differentiates from a gonial cell located more or less centrally within the linear germline clone (Bilinski, 1983).

Krzysztofowicz introduced autoradiographic and histochemical techniques into the studies of oogenesis in Collembola. She showed that besides the ‘canonical’ germ cells actively involved in RNA synthesis, the oocyte is flanked on either side by intermediate cells, originally termed blocking cells, which are transcriptionally dormant and appear to participate only in the transport of macromolecules and organelles from the proper nurse cells into the oocyte (Krzysztofowicz, 1971, 1975).

Another area of Jura’s research interest revolved around germ cell determination and gonad formation. Jura noticed that in *T. bielanensis* the germ cells originate in the 64-cell stage embryo from two to five superficial blastomeres, the first that divide

---

**Fig. 4.** Scanning electron micrographs of the early embryo of *Tetrodontophora bielanensis* (taken by Jura and Krzysztofowicz). (A) An embryo at the transition from 8- to 16-blastomere stage. (B) 16-blastomere stage. (C) A cutaway view of the 16-blastomere embryo showing a central yolk mass (cym) separated from the superficial blastomeres (sb). Scale bars (A, B) 100 µm, (C) 50 µm.
Developmental biology at the Jagiellonian University

Chair at the Jagiellonian University.


melanogaster

Polish zoologist appointed to the Zoology and Comparative Anatomy

investigated embryonic development of weevils and internal
gesis of molluscs and amphibians. Barbara Weglarska for instance

considered heteropteran bugs, and beetles. They explored also embryogen-

tive anatomy, spermatogenesis, oogenesis, parthenogenesis and

Saffman and Lasko, 1999).

and their developmental fate in
cytological and experimental studies on the pole cells formation

tangentially (Jura, 1967a). Using classical histochemical tech-
niques he was however unable to detect any germ cell determi-
nants in collembolan eggs. It would be very interesting to reinves-
tigate this problem using modern molecular markers. Jura’s
cytological and experimental studies on the pole cells formation

Drosophila virilis showed that the destruction of the posterior pole plasm or pole cells by UV
irradiation results in the absence of primordial germ cells but does not disturb the development of the somatic part of the gonad
(Jura, 1964a, b). These findings have been fully corroborated by

Other Smreczynski’s students became interested in compara-
tive anatomy, spermatogenesis, oogenesis, parthenogenesis and
postembryonic development in a wide spectrum of insect groups
including bristletails, dragonflies, stoneflies, homopteran and
heteropteran bugs, and beetles. They explored also embryogen-
esis of molluscs and amphibians. Barbara Weglarska for instance

investigated embryonic development of weevils and internal
anatomy of coccids, but later switched to an entirely different
invertebrate group, the tardigrades (Tardigrada). She provided
first ultrastructural data on the previtellogenic and vitellogenic
growth of the oocytes in Eutardigrada and made important con-
tribution to our understanding of their excretory system (Weglarska,
1979; 1980). She also studied the process of anabiosis in tardi-
grades.

After Smreczynski’s retirement, his student and collaborator,
Czeslaw Jura became the head of the Department (Fig. 5). Under
his leadership, lasting over 20 years, the Department continued
two main research interests initiated by Smreczynski: develop-
mental biology of invertebrates, primarily hexapods (as presented
above), and insect taxonomy. Jura’s collaboration with Professor
Hiroshi Ando (University of Tsukuba, Japan) resulted in publication
of a book ‘Recent Advances in Insect Embryology in Japan
and Poland’ (1987) with many contributions by researchers from
the Department. After Jura’s retirement in 1997, the head of the
Department became Szczepan Bilinski. In 1999 the Department
was split into two units along the research interest. Within the
developmental biology unit, several independent researchers
continued studies of various aspects of invertebrate develop-
ment. In particular, a group led by Bilinski concentrated on the
structure of the ovary and germ cell cluster formation in different
insect groups and its relevance to phylogenetic inference. This
research resulted in a series of papers reviewed in the Biological
Reviews in 1990 and in a special edition of the Folia Histocheni-
et Cytobiologica in 1998 (Stys and Bilinski, 1990; Bilinski, 1998;
Bilinski et al., 1998; Jaglarz, 1998; Kubrakiewicz et al., 1998 a,b;
Szklarzewicz, 1998). Most recently, Bilinski has directed the
group’s research effort towards studies of follicular epithelium
differentiation in insects and, in collaboration with Malgorzata
Kloc (The University of Texas, USA), oogenesis and early embry-
onic development of Xenopus. Bilinski’s outstanding research
achievements and significant contributions to many aspects of
both insect and Xenopus oogenesis merit a separate analysis. In
2005 Bilinski was elected a vice-Rector of the Jagiellonian Univer-
sity and increasingly more demanding administrative duties forced
him to hand down the leadership of the Department to the
assistant professor Teresa Szklarzewicz.

Smreczynski’s legacy continues to influence a new generation
of developmental biologists in the Department of Zoology. They
embark on projects aimed at linking morphological and molecular
features of insect and amphibian oogenesis with their significance
for early embryonic development [e.g. see in this issue Jaglarz et
al. (2008); Pyka-Fosciak et al. (2008)].

Acknowledgement
I am deeply grateful to Professor Czeslaw Jura for generously sharing
with me his extensive knowledge on various facts related to the Depart-
ment history and for providing the photographs. I thank Professors
Czeslaw Jura and Szczepan Bilinski for critical reading of the manuscript.

References


Tissue Res. 179: 401-412.

BILINSKI, S. (1979). Oogenesis in Campodea sp. (Diplura). The ultrastruture of the


Related, previously published *Int. J. Dev. Biol.* articles

See our recent Special Issue *Developmental Biology in Poland* edited by Kloc, Maleszewski and Tarkowski at:


Sclerotome development and morphogenesis: when experimental embryology meets genetics
Anne-Hélène Monsoro-Burq

Mammalian neural tube grafting experiments: an in vitro system for mouse experimental embryology.
D Echevarría, C Vieira and S Martínez

T A Dettlaff and S G Vassetzky

T S Okada

A pioneer of experimental mammalian embryology: Jacques Mulnard.
H Alexandre

Experimental embryology in France (1887-1936).
J L Fischer
Int. J. Dev. Biol. (1990) 34: 11-23