

33rd SYMPOSIUM OF
THE SOCIETY FOR DEVELOPMENTAL BIOLOGY

The Developmental Biology of Reproduction

Edited by

CLEMENT L. MARKERT

JOHN PAPACONSTANTINOU

**The
Developmental
Biology of Reproduction**

THE DEVELOPMENTAL BIOLOGY OF REPRODUCTION

*The Thirty-Third Symposium of
The Society for Developmental Biology*

Athens, Georgia, June 9-12, 1974

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Preface

Recognizing that the continued growth of human populations threatens civilized existence, the Society for Developmental Biology selected the subject of Reproductive Biology as the focus for its 33rd Symposium. Reproductive biology encompasses a very large part of biology; if broadly defined – virtually all of it. This Symposium sought to center attention on basic aspects of reproduction in both plants and animals in the hope of stimulating research that might provide the necessary foundation for effective, practical control of human reproduction. Five areas were selected for emphasis: the formation of eggs and sperm, the activation of the egg to develop into an embryo, the genetic and biochemical events underlying the early development of the embryo, and then, on a physiological level of investigation, the hormonal controls operating in the reproductive process, and the general control of implantation and growth of the mammalian embryo in the uterus. Thirteen reports were given by distinguished researchers in each of these areas and, in accord with past practice of the Society, the international resources of science were used by the inclusion in the Symposium of three investigators from abroad.

In addition to the major scientific reports, one afternoon was devoted to a roundtable discussion of the social and biological implications of controls of reproduction. This roundtable was chaired by Clement L. Markert, with panelists Harriet Presser of the International Institute for the Study of Human Reproduction, Columbia University, and Sheldon Segal of the Population Council, Rockefeller University. The roundtable discussion was recorded on videotape and subsequently edited to produce a 45 minute, 16 mm film for general use by educational institutions and other groups interested in problems of population and human reproduction. One evening of the Symposium was devoted to workshops on a variety of topics related to research in reproduction. The 300 attendees at the Symposium were well accommodated by the host institution, The University of Georgia at Athens. The Society deeply appreciates the excellent organizational support by the local arrangements committee chaired by Stuart J. Coward, and is grateful for the financial support of the National Institute of Child Health and Human Development and the National Science Foundation. This financial support made it possible to bring before the Society a group of outstanding investigators to share their

PREFACE

wisdom and recent research results with those attending the Symposium and now, with the published volume, with a much larger section of the scientific community. All biologists interested in a broad understanding of problems of reproduction will find this Symposium interesting and important for their own work. We hope that the Symposium will contribute, at least in some small degree, to a solution of the most important problem facing human beings today – the control of their own reproduction.

Clement L. Markert

Acknowledgments

The 33rd Symposium was held at Athens, Georgia, June 9-12, 1974. The Society gratefully acknowledges the efficiency of the host committee, the hospitality of the University of Georgia and the support from The National Institute of Child Health and Human Development and The National Science Foundation.

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VIDEOTAPE AVAILABLE ON IMPLICATIONS OF CONTROL OF REPRODUCTION

The round-table discussion on "*Social Implications of Control of Reproduction*" held at our 33rd Symposium in June was videotaped at the Georgia Center for Continuing Education. A 48 minute edited version is now available in color for classroom or other use. The discussion, features Harriet Presser of the International Institute for the Study of Human Reproduction (Columbia University), Sheldon Segal of the Population Council (Rockefeller University), and Clement L. Markert (Yale University).

Methods of birth control are discussed frankly, including the role of abortion as a "back-up" measure. The effect of population control in advanced countries on the balance of world politics is considered and the question of the overproduction of racial groups, such as Blacks, is handled very well. The issue of birth control in the younger group of the population by reversible methods versus permanent methods for older individuals is dealt with in depth. Dr. Markert raised one controversial issue after another for discussion by his distinguished panelists.

The tape is recommended for viewing in college courses introducing reproductive biology to beginning students as well as for showing in more advanced courses on reproduction and developmental biology. It is easily understood by the layman, as well. A small charge for rental will be made and advance booking is recommended. Write Dr. E. D. Hay, Dept. Anatomy, Harvard Medical School, 25 Shattuck St., Boston, MA 02115.

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I. Gametogenesis

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Germinal Plasm and Determination of the Primordial Germ Cells

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I. INTRODUCTION

It appears to be reasonably well established that the functional gametes of many organisms are derived solely from primordial germ cells already present in early embryogenesis. Direct evidence to support this statement has existed for some time in those invertebrate organisms displaying chromosome diminution or elimination (reviews by Wilson, 1925; Gurdon and Woodland, 1968). Equally compelling evidence exists in at least one group of vertebrates, the amphibians, and is based on grafting experiments between genetically marked embryos at the gastrula (Smith, 1964) or neurula stages (Blackler, 1962, 1966, 1970; Blackler and Gecking, 1972a, b). Supportive evidence also has been obtained in the chick (Willier, 1937; Simon, 1957; Reynaud, 1969) and mouse (Mintz, 1960; see also Blackler, 1965).

The idea that the factor(s) responsible for this early germ line determination reside(s) in the cytoplasm traces back to the turn of the century. It is based partly on the demonstrated presence of deeply staining granular

inclusions in the posterior pole plasm of insect eggs, and their incorporation into the early germ cells (review by Hegner, 1914; Wilson, 1925). Hegner (1914) originally considered these polar granules to be the "germ cell determinants", since their destruction resulted in embryos lacking germ cells. The fate of polar granules throughout most stages of the life cycle now has been followed, both in the light microscope (Counce, 1963) and electron microscope (see review by Mahowald, 1971b). Bounoure (1934) was the first to demonstrate the existence of a similar material in vertebrates. He was able to follow the embryonic history of primordial germ cells in the frog *Rana temporaria* by virtue of a specially staining "germ plasm", first identified in the vegetal hemisphere of fertilized but uncleaved eggs. This report has since been substantiated and extended to include a number of anuran amphibians (review by Blackler, 1966). In addition, considerable experimental evidence has implicated the stainable germ plasm in the formation of primordial germ cells (see Smith, 1966; Blackler, 1966, 1970).

Recent emphasis on the germ plasm in vertebrates, largely amphibians, has centered on additional descriptive studies, albeit at the fine structural level. These observations correspond to the earlier work done with *Drosophila*. On the other hand, recent work with *Drosophila* has been concerned with an experimental demonstration of the determinative nature of pole plasm in germ cell formation, considerably extending earlier amphibian work. In this paper a review of this recent evidence is presented both for amphibians and insects, in an attempt to present the "current status" of research concerned with the nature, origin, and function of germ plasm in germ cell determination.

II. FINE STRUCTURAL STUDIES ON GERM PLASM

A. Identification of Electron Dense Bodies Within Germ Plasm

The fine structure of polar granules within the posterior pole plasm in insects was first described by Mahowald (1962) in eggs and embryos of *Drosophila melanogaster*. Subsequent work was extended to other *Drosophila* species and included a description of polar granule morphology during several developmental stages (Mahowald, 1968; 1971a). While the size of the electron dense granules differed in each species (less than 0.5 μm to over 1 μm in diameter), and at different developmental stages, the basic fine structure always consisted of a densely staining fibril, 10 to 15 nm in diameter, which formed an interwoven mesh.

That a structure similar to polar granules might exist within the germinal plasm of amphibian eggs was first indicated by Balinsky (1966). He suggested that granular electron dense bodies observed amidst groups of mitochondria at the vegetal hemisphere of a South African frog egg "may represent the basophilic areas of cytoplasm found at the vegetal pole of amphibian eggs and