NATIONAL ACADEMY OF SCIENCES

# JOSEPH HALL BODINE

*1895—1954*

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*A Biographical Memoir by*

E. J. BOELL

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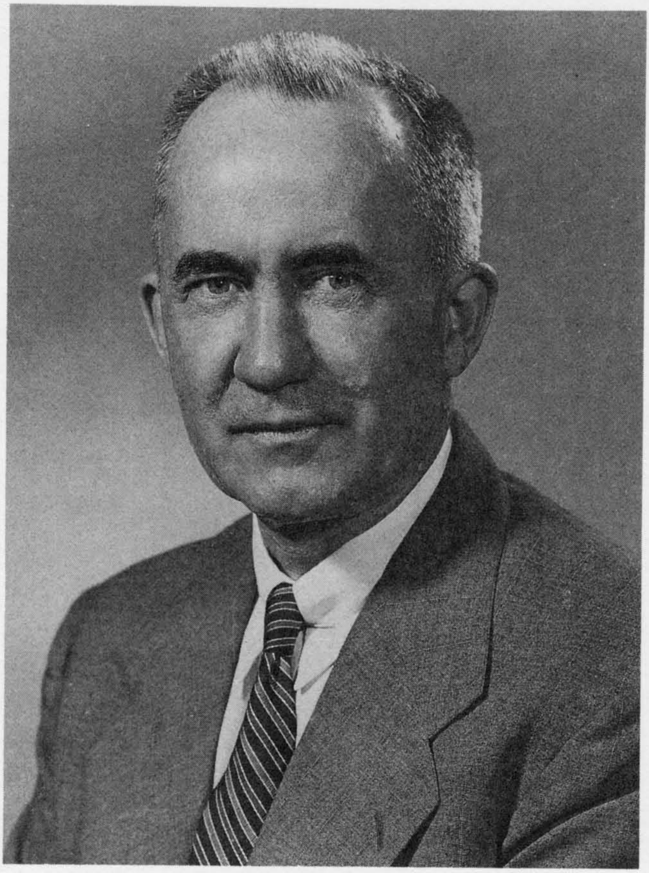

J H Bodine

# JOSEPH HALL BODINE

## *September 19, 1895–July 23, 1954*

### BY E. J. BOELL

JOSEPH HALL BODINE spent most of his scientific life investigating a single organism—the embryo of the grasshopper *Melanoplus differentialis*, and a single process or event—the diapause (or developmental block) that intervenes between two periods of active growth and development. His research work and publications, spanning the period from 1918 to 1953, have made notable contributions to the physiology and biochemistry of embryonic development.

## EARLY LIFE

Joseph Bodine, son of Gilbert and Annie Hall Bodine, was born in Lake Hopatcong, New Jersey, on September 19, 1895. He died in Iowa City on July 23, 1954. Ironically, although he did not smoke and indeed disapproved of the habit, his death was due to lung cancer.

After preparing for college in the schools in Lake Hopatcong, Bodine entered the University of Pennsylvania. He was awarded the B.A. degree in 1915 and enrolled in the graduate school at the University of Pennsylvania immediately thereafter, but his work toward the Ph.D. degree was interrupted by his service in the American Expeditionary Forces. During World War I he served as a captain in the Medical Corps, and he did not receive his graduate degree until 1925.

In his last predoctoral year, Bodine held an appointment as instructor in zoology and, on receiving his degree, was advanced to assistant professor. His promotion to a full professorship occurred in 1928.

Bodine and Sarah Heimach were married in 1919 and had one son, Joseph Hall, Jr. After Sarah's death, Bodine married Eunice Beardsley in Iowa City.

## DEPARTMENT OF ZOOLOGY, THE UNIVERSITY OF IOWA

In 1929, Bodine accepted an appointment as professor and chairman of the Department of Zoology at the State University of Iowa. He served in this position until his death. When he came to Iowa, the undergraduate curriculum in the Department of Zoology was oriented largely toward students intending to continue professional training in dentistry, medicine, or nursing. Graduate work in the Department, except for a vigorous program of teaching and research under the direction of Professor Emil Witschi, was also narrowly focused.

When Bodine accepted the chairmanship at Iowa he received a mandate from the University administration to infuse new life into the Department. What was more, he was given the fiscal support necessary to do so. Accordingly, with budgetary provisions for several new faculty positions over the next few years, appointments were made in protozoology, general physiology, genetics, parasitology, cytology, and embryology, greatly broadening and strengthening the teaching and research activities of the Department.

At about the same time, the Department of Zoology gathered under its wing a struggling biological laboratory on Lake Okoboji in northwest Iowa. With Bodine as director, the Iowa Lakeside Laboratory provided significant new opportunities for graduate teaching and research in the areas of aquatic biology, comparative physiology, and limnology for students at Iowa's Department of Zoology and from other institutions throughout the Midwest.

During Bodine's first years at Iowa, the nation was in the depths of the Depression that followed the 1929 stock market crash. Farm states in the Midwest were particularly hard hit, for this was the time of mortgage foreclosures and bank failures. Tax-supported universities suffered a great deal, for each year there was worry—and not without cause—that already low budgets would be further reduced. In 1930, graduate student teaching-and-research assistantships provided tuition and a stipend of fifty-seven dollars a month. In 1932 the stipend was cut to forty-five dollars. At that time, furthermore, there were no agencies like the National Science Foundation or the National Institutes of Health to supply funds in support of research and graduate fellowships. In spite of this, Bodine always managed to allocate a part of his Department's meager budget to support the research activities of the faculty and their students.

He was, however, a frugal man and insisted that his students construct the apparatus and equipment needed for research from laboratory odds and ends whenever possible, so that being a gadgeteer proved both an asset and a necessity. In 1934 Bodine received a substantial grant from the Rockefeller Foundation to support his research program. Though this ushered in an era of relative opulence, he used most of the funds to make additions to his research staff rather than for equipment, and the habit, developed during the Depression years, of "making what you need for your work" persisted. If, by then, being a gadgeteer was no longer a necessity, it was still an asset.

### *Melanoplus differentialis*

The major part of Bodine's research (and, therefore, that of his students) was devoted to investigating the process of embryonic development within the egg of a grasshopper, *Melanoplus differentialis.* In his publications he emphasized the unique features that make the eggs of this grasshopper ideal for investigating a number of physiological and biochemical aspects of development. One of the most important is a developmental block, occurring naturally without experimental intervention, that interrupts the process of embryogenesis in the egg. This type of block is called "diapause" to differentiate it from the temporary suspensions of growth brought about by adverse environmental conditions.

In the temperate zone, *Melanoplus* females lay eggs throughout late spring and most of the summer. Within the eggs the embryos undergo development for approximately three weeks when diapause intervenes, and growth and differentiation are completely suspended for a prolonged period. In nature, eggs enter diapause in late summer or early fall and remain in the blocked state during the winter months. Thus in the grasshopper, diapause may serve as an intrinsic protective mechanism, insuring that—after an initial short period of growth and differentiation—development will not proceed again until environmental conditions have become favorable for the completion of the process and the survival of the newly hatched nymph.

Grasshopper eggs reared in the laboratory at a constant temperature of 25°C will develop for three weeks and then, even though developmental conditions remain favorable, will enter diapause just as they do in nature. Under such circumstances, the length of diapause in different batches of eggs varies from a number of weeks to several months, but at any time after its onset, diapause can be broken by subjecting the eggs for several weeks to temperatures between zero and 5°C. If the eggs are then returned to a temperature of 25°C, development is resumed and hatching occurs about two and a half weeks later.

Bodine showed that just before and during diapause, and immediately after it is broken (either naturally or by subjecting eggs to low temperatures for an appropriate time), embryos are morphologically indistinguishable. Yet they have strikingly different physiological properties. Whereas the cells of embryos in diapause do not divide, mitotic activity in developing embryos can be observed both before and after diapause. Although the eggs consume oxygen and release carbon dioxide throughout development, these processes occur at greatly diminished rates during diapause. Finally, the respiratory inhibitor, potassium cyanide, has no effect on the oxygen consumption of eggs in diapause but will strongly depress the respiration of developing eggs.

### *The Diapause Factor Theory*

From these data, Bodine developed the theory that, during early development in the egg, diapause is caused by the gradual synthesis of a diapause factor. At a certain stage this factor becomes operative, blocking further growth and differentiation and reducing metabolic activity. He further hypothesized that "a slow, gradual destruction or loss of potency of the diapause factor occurs at constant, high temperatures above developmental zero," and that "diapause factors are extremely sensitive to low temperatures (above developmental zero) and can be completely destroyed or inhibited by appropriate exposure to these temperatures." Because he was unable to determine the nature of the hypothetical diapause factor, how it is formed, and its mode of action, the theory has limited value in elucidating the nature of diapause. It does, however, provide a useful summary of grasshopper development.

### *Oxygen Consumption of Developing Eggs*

Later work showed that the oxygen consumption of developing eggs exposed to a mixture of carbon monoxide and oxygen was reversibly depressed in proportion to the partial pressure of carbon monoxide. By contrast, the oxygen consumption of eggs in diapause was unaffected by carbon monoxide and under certain conditions was actually accelerated. The increased utilization of oxygen proved to be due to the ability of the embryonic cells to oxidize CO to $CO_2$—a property possessed also by the eggs of several other invertebrates and the tissues of various animals.

The depression of oxygen consumption in living cells by carbon monoxide is generally interpreted as due to the inhibition of an integrated system of respiratory enzymes collectively known as the cytochrome-cytochrome oxidase system. The failure of such agents as carbon monoxide and cyanide to depress respiration could mean that either the enzyme system is absent or that, if present, it is not functioning. Quantitative determinations of enzymatic activity and other experimental data point to the latter possibility. The enzyme system is present in diapause as well as in developing stages, but it functions only in the latter. The results thus indicate that during diapause the cytochrome-cytochrome oxidase system is thrown out of gear, so to speak. The enzymes that make up the system are present but not operative. How this occurs is not known, but it is clear that the decrease in the rate of respiration, characteristic of the diapause state, is a consequence rather than a cause of the developmental block.

Between 1934 and 1954, several generations of Bodine's students published the results of a series of quantitative assays of the activity of oxidative and other enzymes throughout development under the general title, *Enzymes in Ontogenesis*. Some of the earliest papers in the series indicated that the level of cytochrome oxidase activity (indophenol oxidase) of diapause embryos was identical to that of developing embryos of the same morphological stage. Only in developing embryos, however, was it evident that the enzyme functions in the process of cellular respiration. During development, owing to the synthesis of new enzyme, the activity of cytochrome oxidase increases. Since this process parallels the transformation of raw materials into the living substance of the embryo, it serves as an indirect measure of embryonic growth. Such enzymes as tyrosinase and cholinesterase, by contrast, reflect the functional differentiation of specific groups of cells or tissues, rather than growth of the embryo as a whole.

These studies, as Florence Moog put it, provided a great deal of information on enzymes as *objects* rather than *agents* of differentiation.

The eggs produced by some animals contain all of the raw materials required for the growth and maintenance of the developing embryos within them. The prime example is the avian egg, which contains within its shell and membranes not only the genetic blueprint and all of the organic and inorganic materials that become elaborated into cells, tissues, and organs of the new individual, but all of the required water as well. An egg of this type has been designated by Joseph Needham as "*cleidoic*" (closed box) to distinguish it from the type of egg that depends upon the environment for everything needed for development except organic materials.

In most respects the grasshopper egg may be regarded as *cleidoic*, though it depends upon the environment for much of the water required for development. In some of his earliest work, Bodine showed that the shell and membranes surrounding the grasshopper egg are permeable, the egg taking up water from the environment by osmotic forces and losing it through evaporation. But with the onset of diapause, water uptake ceases and does not begin again until after diapause has been broken.

In a series of experiments carried out over the course of several years, Eleanor Slifer, one of Bodine's graduate students at Pennsylvania and subsequently a research associate at the University of Iowa, found that water was taken up through only a restricted part of the total egg surface, the micropyle.[1] By covering the micropyles of eggs in which diapause had been broken with an impermeable coating, both water uptake and further development were prevented. In addition, Slifer found that the waxy layer was reduced during the course of diapause and that, when development had resumed after diapause, no trace of the waxy layer could be seen. Slifer then made the exciting discovery that by immersing eggs for a brief period in a fat solvent such as xylol, the waxy layer was dissolved and diapause broken.

This investigation has never been continued, but the available evidence points to the likelihood that diapause is induced by a mechanism—probably genetic in nature—preventing imbibition of water, and that diapause is broken by the destruction of the waxy barrier, thus permitting water uptake and the resumption of development.

## HONORS AND SERVICE TO SCIENCE

At various times in his career Bodine served on a number of important local, state, and national committees: the University of Iowa School of Religion's Board of Control; Iowa Basic Science Board; National Research Council Fellowship Board; Atomic Energy Commission Fellowship Board; chairman, Scientific Advisory Committee, Cold Spring Harbor Biological Laboratory; and Executive Committee, Division of Biology and Agriculture, National Research Council. He was associate editor of the *Journal of Morphology* and, at the time

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[1] E. H. Slifer, "Formation and Structure of a Special Water-Absorbing Area in the Membranes Covering the Grasshopper Egg," *Quarterly Journal of Microscopic Science* 80(1938):437; and "A Simplified Procedure for Breaking Diapause in Grasshopper Eggs," *Science* 107(1948):152.

of his death, was a member of the editorial board of *Physiological Zoology*.

Bodine was a member of various scientific societies including the Iowa Academy of Science, American Physiological Society, American Association of Zoologists (president, 1947), American Microscopical Society, and the Society for Experimental Biology and Medicine. He was a fellow of the American Association for the Advancement of Science and, from 1953, a member of the National Academy of Sciences.

Bodine's research activities covered a span of almost four decades during which the publications from his laboratory enriched the literature of both comparative physiology and developmental biology. As new insights and new techniques became available he returned to old subjects, tackling partially solved problems again and again. As the testimony of his publications shows, Bodine's scientific life could have served as the model for Sir Michael Foster's image of the growth of knowledge, which he likened to "the ascent of a spiral stair from which the observer periodically surveys the same landscape, but each time from a higher level than the last."[2]

I AM INDEBTED to Professor Harold W. Beams of the University of Iowa for providing some of the biographical data and other material included in this memoir.

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[2] This quotation heads the chapter on nutrition in Meyer Bodansky's *Introduction to Physiological Chemistry*, 3rd ed. (New York: J. Wiley & Sons, 1934).

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