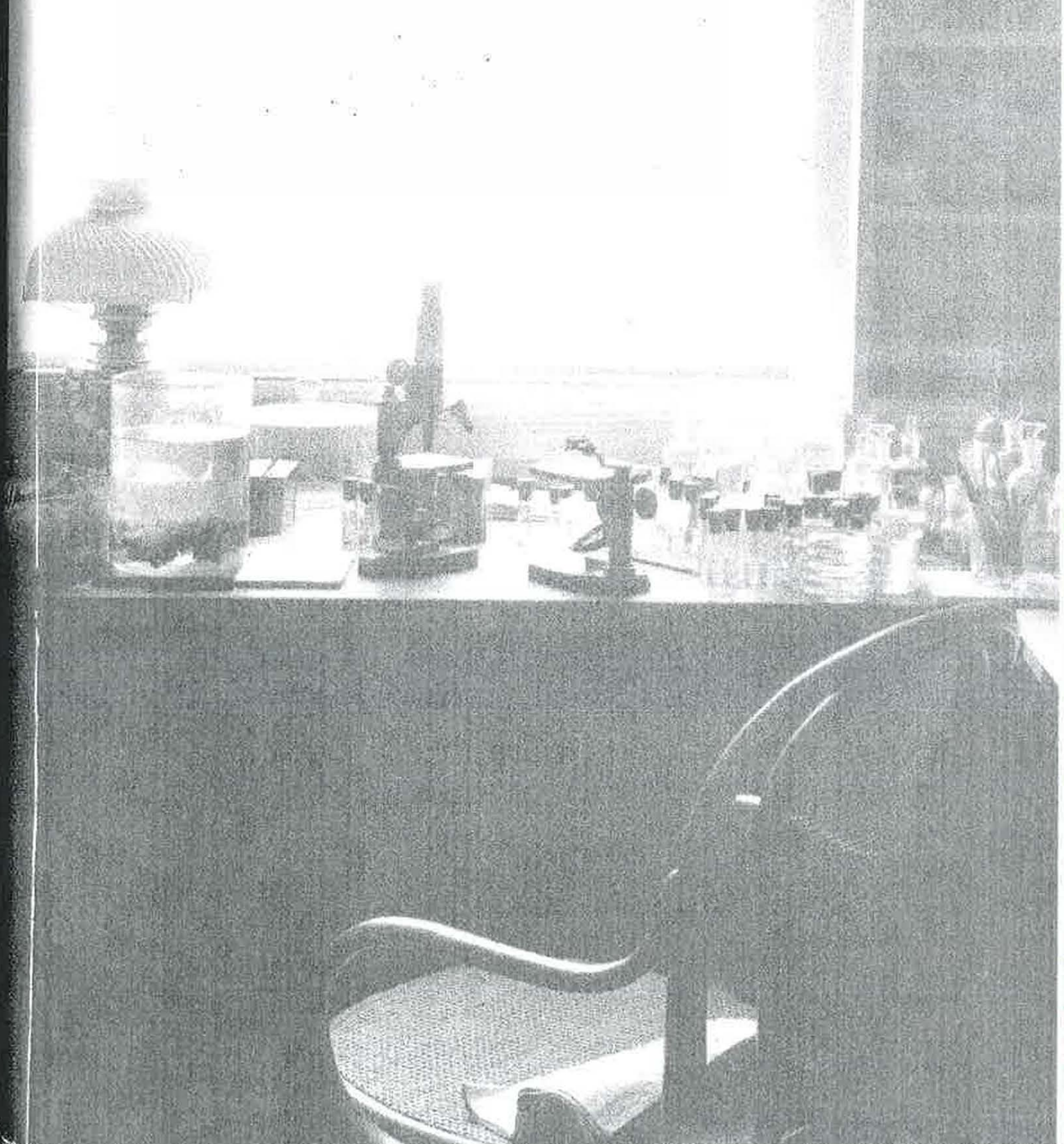
DEFINING BIOLOGY

Lectures from the 1890s

Edited by Jane Maienschein



Printed in the United States of America
10 9 8 7 6 5 4 3 2 1

This book is printed on acid-free paper, and its binding materials have been chosen for strength and durability.

Library of Congress Cataloging in Publication Data

Defining biology.

Lectures given at the Marine Biological Laboratory in Woods Hole, Mass., in the 1890s.
Includes index.
Contents: Introduction / Jane Maienschein—The mosaic theory of development / Edmund Beecher Wilson—The hereditary mechanism and the search for the unknown factors of evolution / Henry Fairfield Osborn— [etc.].
1. Biology—Addresses, essays, lectures.
I. Maienschein, Jane. II. Marine Biological Laboratory (Woods Hole, Mass.).
QH311.D4 1986 574 86-307
ISBN 0-674-19615-5

CONTENTS

PREFACE

Jane Maienschein

The Marine Biological Laboratory in Woods Hole, Massachusetts, offered a series of evening lectures throughout the 1890s. As the first director, Charles Otis Whitman, wrote in his introduction to the published version of those *Biological Lectures*, they played a unique role for biology. By presenting critical issues of the day in general terms accessible to the whole community of researchers, the lectures could bring a much needed cooperative union among the various specialists. Whitman felt that such open interchange of ideas designed to transcend specialization would produce a vital community of American biologists. Indeed, Whitman was right.

These lectures can serve a similar purpose for biologists and historians today. This is, in part, because today's fields of embryology, genetics, biochemistry, cell biology, and behavior studies are the result of research programs pursued at the MBL in the 1890s. These research programs took the United States from a position as distant follower to the leadership role in biology in a very short time early in the twentieth century, and work at the MBL helped make this possible. The MBL provided more than the common root of diverse specializations. It also fostered an intense examination of how those specialized research programs affect and are affected by various broader questions of common interest. Precisely because the lectures addressed general questions and problems rather than presenting detailed research results, the lectures can teach us something about the background of today's specialties, about relations among those specialities, about how they fit into the overall concerns of biology.

The sense of community was important at the MBL and for the emergence of productive lines of research in American biology generally. Researchers gathered in Woods Hole each summer and found a group of people with related concerns, thus allowing them to move beyond the research isolation which most felt at their home institutions. The lecture series reflects the shared interests by addressing overlapping problems: of epigenesis and preformation, of the significance of past evolution, of heredity, of fertilization, of cleavage, of the importance of physiological processes or of environment for directing development. Moving from relatively descriptive cytological work to some manipulative experimental studies in the 1890s, the MBL community sought to understand what happens in development and how differentiation and organization arise and become established.

These *Biological Lectures* achieved a wide circulation through the 1890s within the small biological community, but they have remained relatively unavailable since. This volume of selected lectures should help to remedy that limited availability. The lectures that I have selected for reprinting here illustrate the vitality of the MBL community and center on papers by individuals who were active and thus responding to the shared interests there. Those individuals also served as leaders, by any standards, in biology in the twentieth century. These scientists have in each case recorded their findings and placed them in the context of broader problems of development. I could have chosen other papers or different themes, of course, but this set works to illustrate and demonstrate the importance of the core concerns.

The papers are not what scientists generally consider the "crucial" papers of biology, those which appear to have brought about the major changes in science. Rather, these are the papers which demonstrate the gropings of an important group of scientists at a critical time of change. They illustrate the processes of change and of defining new problems. Most of the problems have not been satisfactorily solved even yet, though biologists have certainly made some progress. Thus, this collection can serve to introduce modern students to some of the central problems of biology, and biologists to that period of scientific work when many of our current best assumptions about what biology should be like were being made.

I wish to thank the librarians at the MBL, especially Jane Fessenden and Ruth Davis, for their enthusiastic help in the preparation of this volume and for their exceptional generosity in providing open access to all materials in their collections. The archivists at the University of Chicago also provided useful materials. All archival passages from both libraries are quoted with permission. In addition, I appreciate the assistance offered at

various stages by Joy Erickson, Richard Creath, and Ernst Mayr. National Science Foundation Grant #SES 85-10359 provided valuable financial support at a crucial time. Above all, it is really the spirit of the MBL from the 1890s which inspired this collection and which lingers still in a few laboratories and in a few individuals.

The photograph of Wilhelm Roux, on page 106, is reproduced courtesy of the Museum of Comparative Zoology, Harvard University, © President and Fellows of Harvard College. The photograph of Charles Otis Whitman, on page 218, is reproduced courtesy of the Joseph Regenstein Library, University of Chicago. All other photographs are reproduced courtesy of the MBL.

INTRODUCTION

Jane Maienschein

The Marine Biological Laboratory opened in 1888, though a bit later than intended. One of the first students, Cornelia Clapp, who was to become a life-long supporter of the institution, arrived on time for the first session only to find carpenters still constructing the new building. No one had made living arrangements for the students; the director had not yet arrived, reportedly because of family illness; and the equipment, donated from the Annisquam Laboratory, remained side-tracked in a railway car somewhere along the way. In short, there really was no laboratory at the specified opening of that first summer session. Yet the students settled into boarding houses; the equipment made its way to Woods Hole; the director, Charles Otis Whitman (1842–1910), and the MBL opened officially on July 17, 1888. Aside from such persistent annoyances as stumbling at night over the many boulders in the paths (unimaginable in today's highly developed Woods Hole setting), that first session proceeded successfully. As Whitman later wrote, the MBL had begun with only seventeen "ids in its protoplasmic body—two instructors, eight students, and seven investigators (all beginners). The two investigators could be likened, with no great stretch of the imagination, to two polar corpuscles, signifying little more than that the germ was a fertile one, and prepared to begin its preordained course of development."[1]

That fertile germ had its origins in the Annisquam Laboratory, directed by Alpheus Hyatt (1838–1902) for the Boston Society of Natural History and the Woman's Education Association of Boston. The Annisquam Laboratory had its roots, in turn, in the Penikese Island school run by Louis Agassiz (1807–1873) and initially stimulated by Nathaniel Shaler

1. Whitman, Address to the MBL Corporation, 11 August 1903, Whitman Collection, MBL Archives.

(1841–1906). As Whitman pointed out repeatedy, the MBL was a lineal descendant of those two ancestors.[2]

The Penikese school was just that, a school. Intended to provide teachers with practical field experience in natural history, it began with financial backing from a wealthy New Yorker, John Anderson, who provided land and funds to build dormitories and laboratory space. Thus the Anderson School of Natural History opened its doors in 1873 to a collection of about fifty school teachers. Agassiz had so many applicants that he had to write to a few whom he had accepted in the early stages and ask them to withdraw in favor of better qualified candidates. The women students were very "schoolma'amy" and the "gentlemen are not a whit behind." according to one newspaper report. The opening proved quite a spectacular and newsworthy event as reporters and guests joined the students in New Bedford for the steamer trip to Penikese Island. Once there, they all celebrated the grand opening with a free picnic and an inspiring informal convocation. Only after the guests had departed for the mainland and the public attention had diminished did the students fully realize that they were on a virtually barren island about two-thirds of a mile long and one-third of a mile wide.[3] Fortunately, their regimen of work kept them sufficiently busy that they had no time to complain.

Some popular accounts give the impression that the students spent their days wandering about the island collecting things willy-nilly. It is true that the instruction was highly individualized, with each student spending a good part of each day exploring, collecting, observing, recording, and generally studying nature rather than books—as Agassiz

2. For discussion of this point see Jane Maienschein, "Agassiz, Hyatt, Whitman, and the Birth of the Marine Biological Laboratory," *Biological Bulletin* 168 Suppl. (1985): 26–34; Ralph Dexter, "From Penikese to the Marine Biological Laboratory at Woods Hole—The Role of Agassiz's Students," *Essex Institute Historical Collection* 110 (1974): 151–161; Dexter, "The Annisquam Sea-Side Laboratory of Alpheus Hyatt, Predecessor of the Marine Biological Laboratory at Woods Hole, 1880–1886," in Mary Sears and Daniel Merriam, eds., *Oceanography: The Past* (New York: Springer-Verlag, 1980), pp. 94–100.

3. For discussion of Penikese see, for example: Elizabeth Cary Agassiz, ed., *Louis Agassiz, His Life and Correspondence* (Boston: Houghton, Mifflin, and Co., 1885), chap. 25; Edwin Grant Conklin, "The Beginning of Biology at Woods Hole: Laboratory at Penikese Forerunner of M.B.L.," *Collecting Net* 2 (1927), no. 2: 1, 3, 6; no. 3: 7; Edward Sylvester Morse, "Agassiz and the School at Penikese," *Science* 58 (1923): 273–275; Albert Hagen Wright and Anna Allen Wright, "Agassiz's Address at the Opening of Agassiz's Academy," *The American Midland Naturalist* 43 (1950): 503–506; "Penikese Island," *Frank Leslie's Illustrated Newspaper*, 23 August 1873, pp. 377–378; Anonymous, *Penikese: A Reminiscence* (Albion, New York: Frank Lattin, 1895), p. 21; E. Ray Lankester, "An American Sea-Side Laboratory," *Nature*, 25 March 1880, pp. 497–499.

urged. But good books, not mere repetitive textbooks, also had their place. So did lectures. Agassiz invited a number of important biologists to address the group on a range of natural history topics. In fact, each day began with structured lectures, followed by an hour or so of dissection. Afternoons often brought freedom to roam and collect, but the evenings were spent attending further lectures, dissecting by candlelight, and then writing up notes from the day's work into the late night hours. Such a system obviously best suited those students capable of framing their own questions and following through with relevant collecting, but Agassiz and his invited speakers also helped to articulate appropriate problems.

The students attending that first year of an American marine school included Whitman and others who later spent time at the MBL, while Alpheus Hyatt reportedly also visited or lectured there.[4] The second summer promised equal success, with some students (including Whitman) returning for more advanced work. Cornelia Clapp (1849–1935) attended that second year, for example. Unfortunately, Louis Agassiz's death late in 1873 and his son Alexander's illness led to the closing of the school after that second year, as much because no one took the initiative to keep it going as for any other reason.

In 1877 Alexander Agassiz (1835–1910) opened his own private laboratory in Newport, Rhode Island, to which he invited an occasional visiting researcher until 1897, when deteriorating water quality forced its closing. Whitman visited there, for example, and began a coordinated project with Agassiz to study pelagic fishes. The younger Agassiz later complained, in refusing to support the MBL, that no one had joined him in providing such facilities for American researchers.[5]

Equally imporant, no one immediately took over the Penikese enterprise of teaching and providing practical experience in natural history. But by 1879 the Woman's Education Association and the Boston Society of Natural History decided that they needed a facility to instruct students, especially women, in this field. The Boston Society appointed Alpheus Hyatt as director and Balfour H. van Vleck (1851–1931), who had been a

4. Dexter, "From Penikese to the Marine Biological Laboratory," p. 161, provides a previously unpublished list of second-year students.

5. George Lincoln Goodale, "Alexander Agassiz (1835–1910)," National Academy of Sciences *Biographical Memoirs* 7 (1912): 291–334. Various documents in the Agassiz Collection at the Museum of Comparative Zoology Archives, Harvard University, such as letters from Agassiz to Hyatt of 30 May and 23 June, 1888, reveal Agassiz's reluctance to support the MBL and other such projects.

student at Penikese, as instructor. The summer school spent two years in Hyatt's house, then moved to a separate location nearby in 1881. There, the Annisquam Laboratory operated as a department of the Boston Society, with the continued support of the Woman's Education Association. This laboratory's purpose was instructional, in line with that of the Penikese school, whereas Alexander Agassiz's laboratory was more attuned to research. Hyatt's ideals helped to direct the lab, as did Van Vleck's particular notions of how to execute instruction. Yet the clear purpose of providing educational opportunities for science teachers and others came from the Boston Society of Natural History, for which Hyatt served as curator.[6]

At times the level of the students' commitment and preparation seemed depressingly low. As Mrs. Hyatt wrote to Alpheus when he was away on an expedition at sea, the group of students was very uninteresting, even tedious. They were essentially raw recruits, hopelessly elementary students, and they were beginning to drive poor Van Vleck to despair.[7] But the school also attracted such men as Thomas Hunt Morgan (1866–1945), who was to become an outstanding researcher and one of the backbones of the MBL.

In 1887 the Woman's Education Association decided that the project had succeeded and no longer need their support. They held the policy of seeding projects until they caught on, and then leaving them on their own.[8] The Annisquam project seemed a success. But Hyatt was tired and wished to develop an American marine laboratory on an independent basis, as an institution separate from the Boston Society of Natural History and from himself as director. He also felt that a new site would prove preferable to Annisquam, which was becoming polluted. Thus came the move to Woods Hole.

The reason for choosing Woods Hole lay largely with Spencer Fullerton Baird (1823–1887). For several years Baird had wanted his friend Hyatt to move his school to Woods Hole, which had purer water, more abundant marine life, a congenial setting, and, not coincidentally, the presence of the United States Fish Commission, which Baird headed. He wanted to build a marine research laboratory at the Fish Commission which would

6. Boston Society of Natural History's *Proceedings* provides discussion of goals and reports of activities.

7. Ralph Dexter, "Views of Alpheus Hyatt's Sea-Side Laboratory and Excerpts from his Expeditionary Correspondence," *The Biologist* 39 (1956–1957): 5–11.

8. Alpheus Hyatt, Boston Society of Natural History *Minutes*, 1887, pp. 3–4.

attract a community of researchers and students; Hyatt's school would prove a valuable complement to this project. Baird did attract cooperation from The Johns Hopkins University, which sent Professor William Keith Brooks (1848–1908) and some students to the Fish Commission, and from Princeton and Harvard. Yet Baird failed to gain the necessary financial support to attract other researchers and to establish a permanent biological research lab in the 1880s at Woods Hole.[9]

In 1887 Hyatt and the Boston Society found Woods Hole attractive indeed. Baird, who had befriended the Annisquam school by sending specimens, had urged a friend to buy land near the Fish Commission, which was held for the benefit of any educational institution that might build there. When the Trustees for the new Marine Biological Laboratory incorporated in 1888, they looked to Woods Hole as their site, and to the Fish Commission for further support.

Hyatt served as the first president of the MBL Trustees and encouraged the group to choose Brooks as the first director.[10] A professor of zoology at John Hopkins, Brooks was clearly one of the most visible of American zoologists. The Trustees hoped that the prestige of John Hopkins might also come with some financial backing from that school. In addition, Hyatt knew Brooks and felt that he might accept the position without salary. Brooks, who headed a small summer school for his own students called the Chesapeake Zoological Laboratory, had developed a working relationship with the Fish Commission and was thus familiar with Woods Hole. Each year John Hopkins had the right to send one or two students to do research there, in exchange for the university's one-time financial contribution to the Fish Commission. Brooks believed in research and wanted his advanced students to have practical laboratory experience. But he never gave any sign that he approved introductory instruction for other than advanced graduate students. The MBL's insistence on teaching as

9. Paul Galtsoff, *The Story of the Bureau of Commercial Fisheries Biological Laboratory, Woods Hole, Massachusetts.* (Washington, D.C.: United States Department of the Interior, 1962); Alpheus Hyatt, "Sketch of the Life and Services to Science of Prof. Spencer F. Baird," Boston Society of Natural History *Proceedings*, 1888, pp. 563–564.

10. MBL *Trustees Minutes* 1 (1888–1897): 11–13. On Brooks: Dennis McCullough, "W. K. Brooks's Role in the History of American Biology," *Journal of the History of Biology* 2 (1962): 411–438; Keith Benson, "William Keith Brooks (1848–1908): A Case Study in Morphology and the Development of American Biology," Ph.D. diss., Oregon State University, 1979; Benson, "American Morphology in the Late Nineteenth Century: The Biological Department at Johns Hopkins University," *Journal of the History of Biology* 18 (1985): 163–205.

well as research and its ancestors' emphasis on providing what Brooks would have regarded as essentially remedial field introductions did not appeal to him. Further, Brooks never became convinced of the wisdom of establishing a second lab in Woods Hole.[11] After some deliberations with MBL supporters, Brooks rejected the invitation to direct the MBL.

Immediately, on May 12, 1888, the Trustees offered the position to the only other American who had directed a biological laboratory—Charles Otis Whitman, then at the Allis Lake Laboratory in Milwaukee, Wisconsin. That unusual lab was founded by Edward Phelps Allis, Jr. (1851–1947), and essentially served as a teaching and research lab for him and a few other researchers. By May 18, Whitman accepted the offer to direct the MBL.[12]

The Woman's Education Association donated its equipment from Annisquam to the MBL and also helped the Trustees raise money for a new laboratory. With Van Vleck serving as first instructor, as he had at Annisquam, the MBL maintained connections with its founders. Yet Hyatt led the Trustees in making it clear that change was also in order, that the laboratory should offer both instruction and more advanced investigation, with instruction taking precedence if the Fish Commission succeeded in establishing itself as a research center.[13] Whitman should develop the lab as he saw appropriate. As Frank Rattray Lillie (1870–1947), Whitman's successor as director, later wrote, this decision worked out well, for in Whitman "the trustees had found a man not only fitted to carry out their purposes but possessing imagination adequate to transform their shadowy ideas, the zeal and determination required to give them form and substance, and the courage to face whatever difficulties might arise."[14]

During those first years, the Fish Commission proved very helpful in sharing specimens, providing seawater, a boat, nets, and so on. And the Fish Commission men (for unlike the MBL group, they were all men) visited and discussed projects. Clapp recorded that Whitman taught basic techniques and how to observe productively and to get results in morphological research. As she enthused about that first year, the year before the appearance of the soon-to-be-famous Wilson, Conklin, or Morgan, "The atmosphere of that laboratory was an inspiration, the days were

11. William Keith Brooks to President Gilman, no date, Gilman papers, Johns Hopkins University Manuscripts.

12. MBL *Trustees Minutes* 1 (1888): 23.

13. MBL *Trustees Minutes* reveal this arrangement in various places.

14. Frank Rattray Lillie, *The Woods Hole Marine Biological Laboratory* (Chicago: University of Chicago Press, 1944), p. 36.

peaceful and quiet; there were no lectures nor anything else to distract the attention from the work at hand."[15]

Although instruction meant introductory lab and practical work such as Agassiz's Penikese school had provided, it did not mean the sort of absolutely elementary work that the Annisquam lab had offered. Students were expected to have some preparation.[16] Thus, in the first years, work concentrated on the structure and life history of invertebrates, with considerable attention also to histological techniques, such as using microscopes, staining, fixing of specimens, and collecting materials to use in teaching. This last technique was important because the students mostly worked as school teachers.[17] Field work and careful observations were clearly emphasized, but so were the latest laboratory methods which could advance the observations. Those students with some training already who wished to pursue individual research projects were encouraged to do so. For the first year, lab work occupied virtually all the time for these independent investigators.

Cornelia Clapp, for instance, had enrolled as a student but was persuaded by Whitman that she had enough experience after her year at Penikese to undertake her own research under his guidance. Thus, she began work along lines Whitman considered important, on cleavage of toadfish eggs. Clapp became sufficiently enamored of research that she decided to take a Ph.D. in biology under Whitman at the University of Chicago, since her Ph.B. at Syracuse University, though satisfactory for her teaching position at Mount Holyoke, had not involved her in such advanced independent research work as she desired.[18]

Students at the MBL could later become investigators or even instructors, as many did in the 1890s and have continued to do. That particular blend of both instruction and investigation, originally endorsed because of the practical need to bring in money to run the laboratory and partly to avoid competition with the Fish Commission, became a life-long commit-

15. Cornelia Clapp, "Some Recollections of the First Summer at Woods Hole, 1888," *Collecting Net* 2 (1927), no. 4: 3, 10.

16. MBL *Trustees Minutes* (1888). Discussion in the Boston Society of Natural History's *Proceedings* 25 (1892): 282–283 reveals the changing climate in education which made the MBL requirement advisable. Teachers were no longer interested in elementary work and general courses by the 1890s, since they had already achieved a higher level of ability.

17. "Trustees' Report," *Annual Report*, 1888, pp. 19–20.

18. "Cornelia Maria Clapp," *Mount Holyoke Alumnae Quarterly* 19 (1935): 1–9. Her first publication from that MBL work appeared as "Some Points in the Development of the Toadfish (Batrachus tau)," *Journal of Morphology* 5 (1891): 494–502.

ment of Whitman's and one for which he had to wage numerous battles with those who would have given up the teaching. As he said in 1898 in his Presidential address to the Society of American Naturalists, instruction at first

> was accepted more as a necessity than as a feature desirable in itself. The older ideal of research alone was still held to be the highest, and by many investigators was regarded as the only legitimate function of a marine laboratory. Poverty compelled us to go beyond that ideal and carry two functions instead of one. The result is that some of us have developed an ideal of still wider scope, while others stand as they began by their first choice . . . On the basis of ten years' experience, and a previous intimate acquaintance with both types, I do not hesitate to say that I am fully converted to the type which links instruction with investigation.[19]

The Trustees' *Minutes, Annual Reports,* and letters reveal considerable debate about the proper role of instruction at the MBL, especially around 1902. But after 1902 it was agreed that some form of instruction would occur. The MBL had established its style and commitments during the 1890s under Whitman.[20]

CHARLES OTIS WHITMAN

The first director of the MBL remains one of the most underrated and understudied of the early American biologists.[21] Always quiet and reserved, to many he appeared far too serious. He was definitely never "one of the boys." Instead, Whitman stood as the stern but gentle and kind father figure for many of the young researchers at the MBL and at the University of Chicago, where he became head of the biology program in 1892. The epi-

19. Whitman, "Some of the Functions and Features of a Biological Station," *Science* 7 (1898): 37–44; MBL *Annual Report,* 1888, pp. 28–29, reveals some of the opposition to instruction; Carol Horgan, Archival Assistant at the MBL, has documented the changing attitudes toward instruction there.

20. W. D. Russell-Hunter, "An Evolutionary Century at Woods Hole: Instruction in Invertebrate Zoology," *Biological Bulletin* 168 Supp. (1985): 88–98, outlines one course of instruction.

21. Frank Rattray Lillie, "Charles Otis Whitman," *Journal of Morphology* 22 (1911): iv–lxxvii; Edward Sylvester Morse, "Charles Otis Whitman," National Academy of Sciences *Biographical Memoirs* 7 (1912): 269–288.

thet "sober and pious Yankee" seems particularly appropriate for this shy and sometimes unhappy man.

The son of farmers, Whitman grew up in Woodstock, Maine. He very soon developed a taste for bird collecting and for roaming through the woodlands near his home, generally preferring his own company to that of others. His uncompromising commitment to principle and the very early whitening of his hair often set him apart as an authority rather than a compatriot for his peers, although he was reportedly a loyal friend. His personality annoyed many throughout his life, but his stubborn refusal to compromise also doubtlessly made it possible for the MBL to develop into the successful enduring institution it became.

After high school, Whitman attended Bowdoin College, receiving his B.A. in 1868 with a largely classical education. Thereafter he served as teacher and principal at Westford Academy in Massachusetts from 1868 to 1872. He also substituted at English High School in Boston during the 1871–1872 school year and received a regular appointment from 1872 to 1875. There Whitman was attracted by Louis Agassiz and signed up for a summer at Penikese in 1873. He had continued his youthful ornithological interests with bird collecting and preparations but had never formally studied or taught natural history or biology. At Penikese, Whitman met Edward Sylvester Morse (1838–1925), who lectured to students on the natural history and embryology of molluscs.[22] Morse, who later played an influential role in obtaining a job for Whitman, was impressed by Whitman's careful and beautiful drawings, a skill for which Whitman received considerable acclaim and which he always cultivated in his own students. Whitman returned for a second summer at Penikese as one of the advanced students.

As Whitman later reported to his student at the University of Chicago, Wallace Craig (1876–1954), he first began scientific work in zoology under Louis Agassiz, but "did not really get under way until he worked with Leuckart on Clepsine in Germany."[23] In fact, the summers at Penikese helped convince him to pursue natural history studies. In particular, the zoology laboratory of Rudolf Leuckart (1822–1898) at the University of Leipzig attracted a number of American students. There Whitman re-

22. "Professor Agassiz's School of Natural History," *Popular Science Monthly,* 1873, 123–124.

23. Wallace Craig, memo to Frank Lillie about Whitman, 29 August 1910, University of Chicago Archives.

ceived his Ph.D. in 1878 for his meticulous study of the early developmental stages of the leech *Clepsine,* a parasitic organism in which Leuckart himself was much interested.[24] His earliest paper addresses suggestions that "precocious segregation" may in fact occur, as Edwin Ray Lankester (1847–1929) and Wilhelm His (1831–1904) had suggested, so that the egg cell already experiences a heterogeneous organization which undergoes "histological sundering" in the course of individual development. That work and subsequent investigation inaugurated the important tradition of cell lineage study at the MBL in the 1890s. As biographer Morse suggested, Whitman reminded "one of a German type of mind" with the meticulousness of that work.[25]

Upon return to the United States, Whitman spent one further year at English High School, then resigned. He applied to The Johns Hopkins University for a special position for graduates as a Bruce Fellow there and received an appointment for 1879–1880, with strong recommendations.[26] Before assuming the fellowship position, however, he left to accept the chairmanship of the biology department at the Imperial University of Toyko, for which Morse had recommended him. With that move he committed himself to a career in scientific research work and teaching in biology.

The Imperial University of Tokyo sought to establish a modern biological department and imported Americans, namely Morse and then Whitman, to direct the program after Thomas Henry Huxley (1825–1895) declined the invitation.[27] In Tokyo, Whitman had four students who completed the program, all four of whom became professors of zoology. Their fond reminiscences upon Whitman's death attest to his influence in Japan. He taught the students the latest histological techniques imported from Germany, he instructed them to draw carefully in order to produce reliable records of their observations, and he introduced them to what it meant to undertake scientific research. One student's later recollections

24. See Klaus Wunderlich, *Rudolf Leuckart* (Jena: Gustav Fischer Verlag, 1978), pp. 41–49, for a list of Leuckart's students; Charles Otis Whitman, "The Embryology of Clepsine," *Quarterly Journal of Microscopical Science* 18 (1878): 215–315.

25. Morse, "Whitman," p. 278.

26. Lillie, "Whitman," p. xix; The Bruce Fellowship, named after Johns Hopkins graduate student Adam Bruce, was established for post graduates to continue their studies in biology (Johns Hopkins University Manuscripts).

27. Lillie, "Whitman," pp. xix–xxiv.

of those days reveals Whitman's influence as well as his views of what good biological work required:

> We had under Professor Morse, only two courses of lecture, general zoology and evolution; and one laboratory work of comparative anatomy. After Whitman became our professor of zoology, Zeiss microscopes and microtomes were newly brought in. A new course in embryology was organized. Each student using his own microscope made experiment of embryology. As we were all rooming in a dormitory, we used to work in the laboratory till twelve at night. Professor Whitman was very industrious in his work, all day long he studied material under microscope. Professor Whitman's office was next to our laboratory and his working table in the office was situated as such that he could see us all, by pushing a door between his office and our laboratory. The door was always kept widely open and as consequence we felt somewhat restrained. At times, he was away, we began to talk and turned the scene quite noisy; but no sooner we have heard his foot step drew near than the noise was gone, stillness reigned again and all students seemed busy peeping microscopes unconsciously . . .
>
> Professor Whitman put much emphasis upon the microscopical study and did not seem to care mere collection of material at random.[28]

Whitman shared his equipment, books, and journals, even helping the students to translate from German and French into English. In Japan, he continued his own research on leeches, examining development and life histories of several species for comparison with his German *Clepsine.*

During the two years Whitman spent in Tokyo, he gained a reputation as the father of Japanese zoology.[29] Yet he left after several skirmishes with university authorities, most notably over publication of his students' papers. By the end of two years, each of his four students had produced a research paper. These Whitman submitted to the university science journal. When informed that only papers by professors could be published

28. Tomotaro Iwakawa, "Professor Charles O. Whitman," trans. Shigro Yamanouchi from the Japanese *Magazine of Zoology* 23 (1911): pp. 2–3, Whitman Collection, University of Chicago Archives.

29. Lillie, "Whitman," p. xx; Whitman, "Zoology in the University of Tokyo," unpublished manuscript.

there and that he should add his name as author to each of the student papers, Whitman's commitment to principle prevailed. He withdrew the papers and submitted them elsewhere. Three appeared in the *Quarterly Journal of Microscopical Science* and the fourth soon appeared in the university journal after all. When his contract expired in August 1881, Whitman declined an invitation to stay and left to return to the United States by way of Europe. As one of his students rather awkwardly reported, despite his conflicts with the university administration, "Professor Whitman loved Japan and sympathized with the Japanese. That his love and sympathy poured forth toward the Japanese in a degree far surpassed than any ever shown by any to us, were marvelously evidenced in the time of Russo-Japanese war."[30]

Before returning to the United States, Whitman stopped at the Naples Zoological Station from November 1881 to May 1882 and worked there as a personal guest of director Anton Dohrn (1840–1909). Officially, a researcher was supposed to be sponsored by an institution and to work at a subscribed table. The United States had taken no subscription when Whitman arrived as the first American at Naples, however, so Dohrn welcomed him as a guest. That Dohrn did not intend to allow this to become standard practice is evident from his insistence that the second American at Naples, Edmund Beecher Wilson (1856–1939), obtain permission to work at some subscribed table or other.[31] At Naples, Whitman studied the dicyemids (parasites of cephalopods), and, following the best standards of the German morphological tradition, he traced the development, life history, behavior, and classification of that form.[32] His careful work well repaid Dohrn's hospitality.

After Naples, Whitman had no job and remained uncertain about whether to pursue the Bruce Fellowship offered two years before at Johns Hopkins. He visited Leipzig for several months, then returned to the United States. There he received an appointment in 1882 as Assistant in Zoology at the Museum of Comparative Zoology at Harvard University, where he remained until 1886.

30. Lillie, "Whitman," p. xxiii for discussion; Chiyomatsu Ishikawa, "Professor Charles O. Whitman," in Yamanouchi, "Whitman," 1911, p. 16, and Katashi Takahashi, "My Old Professor Dr. Charles O. Whitman," 1911, in Yamanouchi, p. 23.

31. Edmund Beecher Wilson to President Gilman, 9 March 1883, student file, The Johns Hopkins University Archives.

32. Charles Otis Whitman, "A Contribution to the Embryology, Life-history, and Classification of the Dicyemids," *Mittheilungen aus der Zoologischen Stazion zu Neapel* 4 (1883): 1–89.

From 1886 to 1889 Whitman directed the Lake Laboratory in Milwaukee to instruct Edward Phelps Allis, Jr., and to conduct biological research. Allis, an independent man interested in biology, had been advised by the British physiologist Michael Foster (1836–1907) to pursue research rather than reading or visiting other people's laboratories. After being tutored for a year by a Johns Hopkins graduate, Henry van Peters Wilson (1863–1939), he sought a different arrangement. Whitman received the highest recommendation, and so Allis invited him to direct a research laboratory where Allis would take part in and learn from the work. Over the Lake Laboratory's eight-year existence, several researchers spent time there and produced published studies, especially in embryology.[33]

His experience at the Lake Laboratory undoubtedly influenced Whitman's life-long hope of establishing an inland "biological farm," as he called it, to complement the marine work of the MBL. His continued failure to convince donors and administrators of the value of such a farm proved a recurring frustration. He wrote in 1895 to Helen Culver, who donated one million dollars for biological work, that he expected her money to fund three projects: biological laboratories at the university, an inland marine station, and a marine biological observatory. The first and third were already organized, he pointed out, and said of the second that "the Experimental Station comtemplated is something wholly new and unlike anything thus far provided for in America or Europe."[34] Somehow the project never came to fruition, and the money all ended up at the University of Chicago rather than at the MBL or an experimental farm.

In addition to the Lake Laboratory itself, Allis also agreed to support the publication of an American journal for zoological work. This journal must remain independent of any particular society and from European direction, Whitman had urged. The *Journal of Morphology* was the result. As Whitman noted in the introduction to that journal, first published in 1897, "The mixed character and scattered sources of our publications are twin evils that have become intolerable both at home and abroad. The establishment of the Journal of Morphology may not be the death blow to these evils; but there is hope that it will, at least, relieve the more embar-

33. Lillie, "Whitman," pp. xxv–xxvii; Ernst J. Dornfeld, "The Allis Lake Laboratory," *Marquette Medical Review* 21 (1956): 115–166, esp. pp. 118–120.

34. Whitman to Helen Culver, 20 December 1885, p. 1, Whitman file, Lillie Collection, MBL Archives. Materials in the Presidential Papers, University of Chicago Archives, contain similar discussions and yet do not clarify what caused the changes of plans for Miss Culver's money.

rassing difficulties of the present situation."[35] Though the journal produced a financial loss for its first years, Whitman managed to persuade the publishers to persist until 1903. After a few years' lapse, the Wistar Institute took up publication again in 1908. In 1898 Whitman also began the *Zoological Bulletin* with William Morton Wheeler (1865–1937), who had worked at the Lake Laboratory and studied under Whitman at Clark University in Worcester, Massachusetts, where Whitman served as chairman of zoology from 1889 to 1892. Intended for shorter articles and reports, the *Zoological Bulletin* was seen as a complement to the *Journal of Morphology*. In 1890, the name changed to the *Biological Bulletin* in accordance with the desire to recognize a general discipline of biological research which combined zoology and botany. The editing and publication moved to the MBL.[36]

In 1889 Whitman had hoped to receive an appointment at Columbia University, but did not.[37] Instead, he went to the newly opened Clark University, whose graduate research orientation appealed to Whitman. He quickly began to attract his own students, who went with him to the MBL for summer work. Unfortunately, Whitman was one of many Clark faculty members who soon experienced displeasure with the administration over various issues. In 1892 he and others left Clark to become the distinguished core of the new University of Chicago biology program. The brief Clark stay was nonetheless important for Whitman. During those three years he was simultaneously interpreting for the department there, for the MBL, and for his journals and lectures series what biological work should be like, what problems were important, what methods were appropriate, and which investigators should be encouraged. He had tremendous influence in those years over the shape of American biology, with little competition except from Johns Hopkins. And the best students from Hopkins all found their way to Woods Hole and fell under Whitman's influence to some degree as well. His net of connections was spread wide, and loyal students such as Frank Lillie followed him from Clark to Chicago and to the MBL and back. Investigators at the MBL returned year after year and assumed leadership roles there at Whitman's request. MBL researchers published in the *Journal of Morphology*, the *Biological Bulletin*, and the

35. Lillie, "Whitman," p. xxvi.

36. The prospectus for each journal reveals the differences in goals.

37. Whitman letters to Alexander Agassiz, Agassiz Collection, Museum of Comparative Zoology Archives, Harvard University.

Biological Lectures series. Biology remained a small field prior to 1900, and Whitman exerted a powerful influence on most of the American researchers.

WHITMAN'S IDEALS FOR BIOLOGY

It was at the MBL that Whitman most directly revealed his ideals for American biology and most successfully played them out. In his *Biological Lectures* series, his *Annual Report to the Corporation*, and his letters to friends and colleagues he articulated his hopes and frustrations. "Specialization," "cooperation," and "independence" served as Whitman's watchwords for biology.

In his inaugural lectures for the *Biological Lectures* series in 1890, Whitman insisted that specialization was desirable, indeed necessary for biology. No one investigator could manage all of biology any longer. Specialization and organization had become "companion principles of all progress" and "the most important need of American biology," according to Whitman. American biology lagged far behind German work, he had lamented in 1889, partly because of the failure to specialize and cooperate.[38] People fear specialization, he acknowledged, but proper understanding could bring acceptance. Essentially, specialization in science was an expression of the principle of division of labor which societies of individuals all experience. Individual cells, he said, begin as independent units, each nearly like the others. Progressive development brings specialization, with mutual dependence, and resulting social organization. Division of labor brings union of the laborers, with the individual parts continually responding to their places in the whole. There is no pre-existing structure which determines what each individual cell (or person) shall become, but hereditary potentials influence the particular division of labor that occurs within the system. With higher degrees of specialization and organization comes higher rank in the "scale of life and intelligence," since organization depends on each part's sense of place in the whole, and knowledge of the whole presupposes knowledge of the parts as well. Some fear division of labor because they fear that the body—or science or whatever—will disintegrate into unrelated parts, but "there are centripetal forces that keep pace with the centrifugal ones; and the danger of any

38. Also discussed in Whitman, "Biological Instruction in Universities," *American Naturalist* 21 (1887): 507–519.

science flying into disconnected atoms is about as dreamy and remote as the dissolution of the earth itself."[39]

Specialization tends to run ahead of organization, so researchers must work cooperatively to keep organization in sight. A permanent national marine biological station, presumably the MBL with a solid financial basis and truly national support, would enhance this essential cooperation and organization by bringing together various specialists. Such a station was "*the* greatest desideratum of American biology."[40] The ensuing efforts to secure a solidly founded national station while ensuring independence from any one agency, university, or individual earned Whitman considerable heartaches and ultimately led him to withdraw from MBL administration. The move toward specialization without cooperation, and the insistence on analytical study of parts and not the whole in biology, similarly discouraged the idealistic and optimistic Whitman. Yet he persisted throughout the 1890s in pushing his ideas into effect.

In his second lecture to the MBL, also in 1890, Whitman elaborated what he saw as current specialty areas of research. Some seek to establish geneological relationships and a system of classification; others examine those forms that exist now. Comparative anatomy, paleontology, and embryology all work in parallel to find homologies, for example. Similarly, geological succession and embryological development, zoological gradations, and geographical distribution of animals also are parallel phenomena, each revealing the community of descent. Study of each runs parallel to study of others. Each informs the others. For any topic of research, one would have begun "with a special problem and found it to be the centre of inquiries, leading in all directions into the unknown. So it is with all special subjects in biology. The farther we pursue them the broader and more interesting they become. Nothing could be farther from the truth than the idea that such questions are isolated, and devoid of interest to all except the specialist."[41]

Even morphology and physiology, thought by many to represent two distinct and even divergent research traditions, were two aspects of the same thing, in Whitman's view. While one studies form, the other studies function of the same organism. Physiologists have ignored important problems such as the fundamental processes of heredity, variation, and

39. Whitman, "Specialization and Organization," 1890, p. 22.
40. Ibid., p. 24.
41. Whitman, "The Naturalist's Occupation," 1890, p. 52.

adaptation, and morphologists have only just begun to address some of the physiologists' traditional questions. Physiologists must learn to appeal to paleontology and especially to embryology as sources of evidence, because "the embryological series, often including free larval stages, furnishes one of the grandest fields for experimental study. Here the physiologist has an opportunity not only to study by experiment but also by direct observation and inference, and thus to join hands with the morphologist both in methods and results."[42] Thus, at the MBL Whitman developed a department of physiology in 1894, headed by Jacques Loeb (1859–1924), whom he imported from the University of Chicago. From the beginning the MBL included botany as well as zoology, though the latter clearly maintained its primacy. He also introduced new courses as they seemed of sufficiently general interest and substance.

Despite Whitman's stature as a leader of American biology, battles at the MBL over money and control of the laboratory climaxed in 1897 and 1902 and led to his discouragement and eventual withdrawal from his influential post there.[43] Though Whitman remained the official head of the MBL until 1908, he discontinued publication of the *Biological Lectures* in 1900 and of the *Journal of Morphology* in 1903, and in effect withdrew from the MBL and the University of Chicago after 1902, relinquishing control of the MBL to his assistant, Lillie, who became the official director in 1908.

Whitman had by that time returned to his beloved birds, concentrating on the evolution, behavior, and development of pigeons. His unhappy family life, including his apparent estrangement from his wife, Emily Nunn, and his difficulties with a pathologically shy and troubled son, led him increasingly to communion with his pigeons.[44] Indeed, his final paper to the MBL in 1898 on animal behavior is probably Whitman's masterpiece. As his biographer, Morse, said of that lecture, which he evidently heard,

42. Whitman, "General Physiology and Its Relations to Morphology," *American Naturalist* 27 (1893): 802–807. From the "5th Annual Report of the Director," MBL (1892).
43. Whitman to confidant Edwin Grant Conklin, a series of letters, Whitman Collection, MBL Archives.
44. Whitman's friends systematically avoided discussion of his family problems, as revealed in Lillie Collection, MBL Archives, and Whitman Collection, University of Chicago Archives. Pieces of letters hint that major problems existed, for example, Ishikawa, "Whitman," 1911, p. 18, reports that Mrs. Whitman and their son were not living with Whitman when Ishikawa visited in 1908. Letters from Mrs. William Keith Frost to Lillie, Whitman Collection, University of Chicago Archives, provide evidence of Whitman's frustrations.

> Dr. Whitman gave one of his most interesting and delightful essays. The table of contents even is as enjoyable as the menu of a rich feast. The lecture is crowded with facts which reveal his wonderful powers of observation. General considerations regarding the origin of instinct, which he shows precedes intelligence, and weak points in the habit theory, etc., indicate his thorough knowledge of the various discussions which have been published. In short, a fair presentation of this luminous lecture would be impossible in this brief memoir. It may stand as a model for discourses of this nature.[45]

That work is supplemented by the posthumous publication of three impressive volumes on pigeons, painstakingly and loyally undertaken by Oscar Riddle (1877–1968), Whitman's student at Chicago who carried on Whitman's pigeon work, indeed carried on with Whitman's own pigeons after Whitman's unexpected death in 1910. Yet Whitman and his studies of pigeon evolution had come to be regarded as old-fashioned at the University of Chicago by this time. When Riddle took up the work, he was effectively instructed to leave Chicago.[46]

Whitman had been caring for his avian friends in their coops in his backyard during a sudden cold spell in Chicago in November 1910. He developed pneumonia and died shortly. Though his helpful assistant, Lillie, officially took over the Chicago department as well as the MBL, it became clear that Lillie did not share all of Whitman's commitments. He did nothing to help Riddle, for example, though Whitman had promised Riddle an official faculty position upon his return from a research visit to the Naples Zoological Station. Riddle received word that Lillie would not honor Whitman's commitment, partly because of departmental sentiments, and it was only through the intervention of Whitman's friend Albert Prescott Mathews (1871–1957), a physiologist, that Riddle obtained sufficient funds to remain in Chicago and to keep the pigeon colony alive for another year. The next year, Riddle and Whitman's pigeons departed Chicago for the Carnegie Laboratory at Cold Spring Harbor, a symptom of

45. Morse, "Whitman," p. 278.

46. Oscar Riddle, ed., *Orthogenetic Evolution in Pigeons* (vol. 1), and *Inheritance, Fertility, and the Dominance of Sex and Color in Hybrids of Wild Species of Pigeons* (vol. 2). Harvey A. Carr, ed., *The Behavior of Pigeons* (vol. 3) (Washington, D.C.: Carnegie Institution, 1919). Takahashi, "Whitman," 1911, pp. 24–25, reports that Whitman asked him repeatedly to stay and work on the pigeons since Whitman needed assistance. Whitman reportedly was spending most of his salary ($7,000) and most of his time on the pigeons.

the erosion of support at Chicago for Whitman's program of behavioral research and for his ideas about biology.

LEADING PROBLEMS: PREFORMATION AND EPIGENESIS

Despite the loss of support in the 1900s, Whitman's ideals played a major influential role in shaping American biology in the 1890s. The very idea of having a series of biological lectures to address central issues of the day, as well as the particular speakers and subjects chosen, reveal Whitman's personal stamp.

The focus of interest of the *Biological Lectures* shifted from year to year as new discoveries brought new questions, but some themes underpinned discussion throughout the 1890s. Most notably, questions about the significance of heredity and evolution for development, and related questions about the significance of cell cleavage for differentiation of individuals, ran through many of the lectures. Initially, discussion centered on the question, to what extent is the egg cell already organized in its earliest stages? Is there something brought to the egg by heredity, something to some extent predelineated? Or does form and heterogeneity emerge only gradually or epigenetically in the course of time? All of these discussions directly impinge on the more general debates about preformation and epigenesis. Those debates, revived on the continent in the 1880s and 1890s, also found expression at the MBL.[47]

To understand the debates, the modern reader must recognize that American biologists in the 1890s regarded preformation and epigenesis as closely associated with heredity and development, respectively. But they did not simply identify preformation with heredity and epigenesis with development. Rather, they saw both heredity and development as more complex. They did not even neatly distinguish heredity from development as biologists generally do now. Heredity did *not* generally mean transmission of characteristics or packets of information, after which development took over. Instead, heredity concerned whatever was passed from parent to offspring, and was regarded as a morphological phenomenon. Development of the individual involved its continuous response to the surrounding environment and acted as a physiological process with a morphological basis. Development of species paralleled development of

47. Jane Maienschein, "Preformation or New Formation—Or Neither or Both?" in T. J. Horder, J. A. Witkowsky, and C. C. Wylie, eds., *A History of Embryology* (Cambridge: Cambridge University Press, 1986), discusses the debates more generally.

individuals. Hyatt, in his only lecture to the MBL, in 1899, pointed out that heredity and reproduction both involve "the production of like by like."[48] The Americans generally believed that heredity accounts for similarities of form, while ontogeny brings variations. Both heredity and development act throughout an individual's life, and neither traditional preformation nor epigenesis strictly accounts for individual differentiations and development.

August Weismann (1834–1914) provided the favorite point of attack for the Americans. He offered a neat, apparently preformationist, view of individual development, suggesting that hypothetical units (the biophores, ids, idants) transmitted physical substance and thereby characteristics to offspring and on into individual cells. Elaborated by Wilhelm Roux (1850–1924), and seen in part in the introduction to his *Archiv für Entwickelungsmechanik der Organismen*, translated by William Morton Wheeler and reprinted here, was the Weismann–Roux hypothesis of qualitative cell division. That hypothesis held that the initial pool of determinants was, in the course of development, divided into a mosaic of different cells. Each of these then developed and became differentiated autonomously, according to its internal materials. Throughout the 1890s, the Americans rejected Weismann particularly, and the Weismann–Roux hypothesis, as too simplistic, too speculative, inadequate, and ad hoc. Indeed, Mathews expressed the common view when he indicted such theories as a "scientific misdemeanor."[49]

In 1890 Henry Fairfield Osborn (1857–1935) addressed the MBL on "Evolution and Heredity" and pointed out the tendency of researchers to embrace incompatible ideas. Evolution seemed to progress not randomly but along certain lines, as the neo-Lamarckians had shown. Strictly fortuitous variations would encounter the problems of swamping and regression. Thus, some version of inheritance of acquired characteristics seemed indicated. Yet Weismann's theory of the continuity of the germ plasm rejected such a possibility. The evolutionary process requires some theory of inheritance, Osborn held; indeed, explaining the "how, why, and when of variations" would furnish a "crucial test for any heredity hypothesis." Osborn believed that the evidence proved that Weismann's

48. Iris Sandler and Laurence Sandler, "A Conceptual Ambiguity that Contributed to the Neglect of Mendel's Paper," *History and Philosophy of the Life Sciences* 7 (1985): 3–70.
49. Albert Prescott Mathews, "The Physiology of Secretion," 1899, p. 183.

preformationist hypothesis of germ plasm continuity was severely problematic and inconsistent with other facts, but he nevertheless urged openmindedness and a "liberal and generous spirit of discussion."[50] How far heredity acted and when individual developmental responses to environment took over remained open questions for Osborn.

In 1893 the University of Pennsylvania botanist William Powell Wilson (1844–1927) insisted that both internal and external conditions cause variations. Thus, variations arise in part because of environment and are thereafter neatly reproduced in the offspring. Heredity and developmental plasticity in response to environmental conditions work together to explain variation; hence, neither preformation, closely associated with internal factors, nor epigenesis alone prevails.[51]

E. B. Wilson directly addressed "The Mosaic Theory of Development" in his lecture of 1893 and also called explicitly for something of a compromise between traditional preformation and epigenesis. Embryologists had moved beyond the old biogenetic law, which stated that an individual's ontogeny recapitulates its phylogenetic past. Though no embryologist would any longer hold that the individual actually exists as such in the egg, recent events had brought a move for some toward a version of preformation. For these new preformationists, structural units collect in the idioplasm of the germ cell to produce something of a microcosm of the future organism, Wilson pointed out. Such a microcosm theory of particulate inheritance began with Darwin and had been "pushed to its uttermost logical limit by Weismann," in Wilson's opinion. The mosaic theory of Weismann and Roux maintained that the causes of differentiation are mechanical and lie within the egg itself, carried out through cell division. Yet, "brilliantly elaborated and persuasively presented as they are, they do not at present, I believe, carry conviction to the minds of most naturalists, but arouse a feeling of scepticism and uncertainty; for the fine-spun thread of theory leads us little by little into an unknown region, so remote from the *terra firma* of observed fact that verification and disproof are alike impossible." The facts of experimental embryology had dealt a death blow to the mosaic theory, Wilson felt, and thus "we have found good reason for the conclusion that the mosaic theory cannot, in its extreme form, be maintained." Yet neither could he accept the extreme epigenetic

50. Henry Fairfield Osborn, "Evolution and Heredity," 1890, p. 141.
51. W. P. Wilson, "The Influence of External Conditions on Plant Life," 1893, p. 165.

views of Hans Driesch (1867–1941) and Oscar Hertwig (1849–1922). Instead, he concluded that ontogeny begins with an egg, which already has some definite constitution and is thus not raw, homogeneous matter, while each step thereafter depends also on the interaction of the parts of the organism. Therefore, something of internal or apparently predelineated self-differentiation but also something of responsive, regulative, and hence epigenetic adjustment directs ontogenetic development. Initial organization is transformed into new organization through cell division and influenced by cell interaction.[52] This compromise position received further articulation with John Ryder's and Whitman's lectures of 1894 and achieved its greatest degree of clarity with William Morton Wheeler's lecture of 1898 (reprinted here).

The 1894 series of lectures in which Whitman expressed his own views about preformation and epigenesis appears as a coordinated effort to compare different points of view, to air varying opinions. "Cross-fertilization works rejuvenation in theories as in organisms," Whitman wrote in his prefatory note to that volume (published in 1895). Attacking the excesses of the neo-epigenesists, he noted that "an epidemic of metaphysical physics seems to be in progress—a sort of *neo-epigenesis*."[53] Clearly Whitman had no sympathies with those moves toward epigenesis which rejected the importance of heredity altogether. Though he did not explicitly say so by 1894, he may well have begun to regard such work as Loeb's mechanistic studies of development as at times bordering on such excesses, despite their provocative creativity. By 1894 Loeb had begun to publish his work on artificial stimulation of cell division and production of multiple embryos, followed by similar experiments and arguments for epigenesis by Morgan and Driesch, among others.[54] As Loeb had said in his lecture of 1893 and elsewhere throughout his work, all life phenomena are determined by chemical processes. Differences in growth result from different amounts of energy or differences in resistance to energy, since energy is used to overcome resistance and produce growth. Therefore, differences in form can be explained in terms of the chemical differences which account for differences in resistance to growth. The extent to which the external conditions acting on the egg can alone explain development,

52. Edmund Beecher Wilson, "The Mosaic Theory of Development," 1893, pp. 3, 5, 9.
53. Whitman, "Prefatory Note," pp. iv–v.
54. For discussion of Loeb's work, see Philip Pauly, "Jacques Loeb and the Control of Life: An Experimental Biologist in Germany and America, 1859–1924," Ph.D. diss., Johns Hopkins University, 1980.

without appeal to ancestral evolutionary conditions, remained a very heated issue in that year.[55]

In his rejection of extreme epigenesis, Whitman did not endorse traditional preformationism either. Development begins with something, something which is a product of the historical past and is influenced by heredity. That something is neither of the traditional alternatives, however; it is neither strictly performed nor homogeneous. One must avoid being sucked into the Charybdis of extreme preformation as surely as one must steer clear of the Scylla of extreme epigenesis. The real question for the day, Whitman clarified, was no longer preformationism or epigenesis. Rather the modern biologist should ask: "How far is post-formation to be explained as the result of preformation, and how far as the result of external influences?"[56] The germ is already organized in some way and yet external conditions exert an influence. How do the two work together, with what differential emphasis on each?

The embryologist John Ryder (1852–1895), who had directed the United States Fish Commission Laboratory in Woods Hole in 1888, expressed a view with a different emphasis in his discussion of "A Dynamical Hypothesis of Inheritance" in 1894. There he baldly asserted that Weismann's and other preformationists' theories were simply wrong. One must dismiss all such "imaginary corpuscles" as Weismann's and look to the mechanics and dynamics of development. The focus on ids and such presumed determinants "time will show to have been about as profitable as sorting snow-flakes with a hot spoon."[57] The ids are simply passing shadows, effects rather than causes of anything. Instead, the molecular, chemical organization of the egg (which is inherited) and the reciprocal influence of cells on each other, with energy as the only motive force, will explain development and heredity. Variations occur, on this view, as molecular systems interact with systems in the environment. The initial egg is neither preformed nor perfectly isotropic, according to Ryder. Rather, epigenetic development begins with a dynamically organized egg since it has a "determinate ultramicroscopic molecular mechanism."[58] Epigenesis with dynamic determinism: Ryder's lecture reveals the unsettled state of discussion of heredity and development, of preformation and epigenesis.

55. Jacques Loeb, "On Some Facts and Principles of Physiological Morphology," 1893, esp. p. 54.
56. Whitman, "Evolution and Epigenesis," 1894, pp. 221, 223.
57. John Ryder, "A Dynamical Hypothesis of Inheritance," 1894, p. 25.
58. Ibid., pp. 33, 28, 51.

Wheeler, in his lecture of 1898, brought a considered perspective on the debates, explaining the persistence of both epigenetic and preformationist viewpoints in terms of personality differences. Some found it easier to pass from the simple to the complex, to envision complex form as emerging from relative homogeneity. "The physiologist, who deals with processes, who is ever mindful of the Heraclitean flux, inclines naturally to" epigenesis, Wheeler wrote. "On the other hand, he who readily idealizes and schematizes, whose mind is endowed with a certain artistic keenness, an appetite for forms and structures, and a tendency to make these forms final patterns, eternal molds, more permanent than the substance that is poured into them—such a one will find more difficulty in understanding *how* the homogeneous can become the heterogeneous."[59] This latter is the morphologist, the Platonic preformationist. It is not clear which will prove to have the viewpoint more in accordance with the facts. Instead, agreeing with E. B. Wilson and Whitman, Wheeler suggested that the eventual resolution would lie somewhere between the extremes:

> The pronounced "epigenecist" of to-day who postulates little or no predetermination in the germ must gird himself to perform Herculean labors in explaining how the complex heterogeneity of the adult organism can arise from chemical enzymes, while the pronounced "preformationist" of to-day is bound to elucidate the more elaborate morphological structure which he insists must be present in the germ. Both tendencies will find their correctives in investigation.[60]

The ongoing discussion of preformation and epigenesis pointed toward the related issues of heredity and development, internal self-differentiating factors and external environment, and the significance of cell division. Such issues also underlay much of the discussion at the MBL in the 1890s and thus provide a background for the public evening lecture series. A closer look at those lectures, year by year, will reveal shifts in the assumptions and in the focus of discussion against a background of concern about the extent to which individual development is conditioned by inherited, internal, and hence preformed factors or by internal physiological responses to changing environmental conditions.

59. William Morton Wheeler, "Caspar Friedrich Wolff and the *Theoria Generationis*," 1898, p. 282.
60. Ibid., p. 284.

LEADING PROBLEMS: CHANGES THROUGH THE 1890s

The *Biological Lectures* certainly did not settle all questions about the relative importance of environment or internal conditions, of development or heredity, of epigenesis or preformation. But they did set out various alternative views of the issues and helped to clarify the points of disagreement and possible avenues for resolving disagreements.

Intimately connected with the questions about what directs development was work on cell organization and cell cleavage, pursued through cell lineage study and through investigations of fertilization. Many of these studies were undertaken with the purpose of providing solid data to address the value of particular working hypotheses about the nature of development. Specifically, the concern about the extent to which the egg is already organized at an early stage and what makes it differentiate further, which had a central part in the epigenesis and preformation discussions, appeared here as well.

1890 In fact, developmental concerns really lay at the core of the MBL discussion, as is evident even from the lecture titles through the 1890s. But development included heredity and evolution, so excluded relatively little. The first year's lectures, in 1890, reveal a traditional interest in the German morphological program. Thus, E. B. Wilson addressed "Some Problems of Annelid Morphology," for example. Using the opportunity to consider some general morphological issues, Wilson pointed out that the primary question concerned the derivation of the vertebrates. Taking Darwin's theory of common descent as a "splendid working hypothesis," the morphologist then had two questions: first, "What is?" and second, "How came it to be?"[61] Every question of morphology is also a geneological or historical inquiry, therefore. Since we can no longer see the actual ancestral forms, we must appeal to lower invertebrates and look for similarities which may reveal the parental characteristics. Three such noteworthy similarities include metamerism (or the production of segments), apical or unidirectional growth (at one end only), and concrescence (or the union of two halves along the median line). The origins and significance of these similarities remain unclear, Wilson concluded after reviewing the evidence. Only concrescence even appeared to be under a "satisfactory working hypothesis." But biologists should not despair because of the lack of positive results, Wilson urged. The good scientist must also pursue unsolved problems of the deepest interest such as these.

61. E. B. Wilson, "Some Problems of Annelid Morphology," 1890, p. 54.

Indeed, the "present need is for new facts, not for new theories. When the facts are forthcoming, the theories will take care of themselves." Wilson was himself embarked in 1890 on a detailed cell lineage study of the annelid worm *Nereis* and hoped to obtain sufficient descriptive data to shed light on questions of homology, ancestral forms, and such problems of morphology.[62]

Similarly, in 1890 assistant professor of zoology at Clark University John Playfair McMurrich (1859–1939) cited the value of explaining the origin of the metazoa from lower organisms. Ernst Haeckel's (1834–1919) gastraea theory of 1872 stood as the standard, suggesting that a monerula gave rise to a cytula, then to a morula, planoea (blastular form), and gastraea, after which the metazoa branched off. Haeckel's theory suffered from errors, so that various alternatives had arisen, several of which McMurrich discussed. Clearly the gastraea had never even existed, he maintained.[63] The important point here is that McMurrich, like Wilson, was presenting a problem, discussing evidence and alternative theories, then concluding that what biology most needed was more data and more study, in this case of the early development of invertebrates. As with Wilson's work, McMurrich reveals a traditional morphological perspective with an additional emphasis on careful observation and study and rejection of clever, neat theories that do not accord with the facts.

Osborn, Edward Gardiner Gardiner (1854–1907), and Morgan also addressed problems typically within the morphological tradition in that volume of 1890, Osborn looking at the relation of heredity (and stability) to evolutionary change, Gardiner at theories of death, and Morgan at phylogenetic relationships of sea spiders. Morgan's lecture was the most traditionally morphological and reveals a side of his work as a budding biologist that historians have usually overlooked. The lecture by Shosaburo Watase (1862–1929), "On Caryokinesis," reflected his study with Whitman at Clark University, for there Whitman had addressed the problem of Oökinesis. Watase's interest in the cell and cell changes and movements through early development shows the direction toward which work at the MBL soon moved, encouraged by Whitman—namely, toward careful analysis of early developmental changes.

1891 and 1892 Lectures for these years never appeared in print, but the

62. Ibid., p. 78; Edmund Beecher Wilson, "The Cell-lineage of Nereis: A Contribution to the Cytogeny of the Annelid Body," *Journal of Morphology* 8 (1893): 579–638.

63. See Ernst Haeckel, "Gastraea-Theorie," *Jenaische Zeitschrift* 8 (1874). 1–55; John Playfair McMurrich, "The Gastraea Theory and Its Successors," 1890, pp. 97, 91, 106.

Annual Reports record contributions to the series, nevertheless. In fact, even in the published years some lectures were not included in the volumes. In some cases, archival materials show that lecturers simply did not submit papers. Other lectures did not cover topics relevant to the series, though they undoubtedly appealed to the public audience. Morse's discussions of China and Japan fall into this category, as did some of the more descriptive and general discussions of evolution. For 1891 and 1892 Whitman had no publisher; only for the 1893 series did Ginn and Co. take over publication of the series.

1893 The second published volume of lectures came only in 1893, then, three years later. Those three years were very important ones, for in the meantime Weismann, Roux, and Driesch had been at work articulating theories and advocating a new experimental approach to embryology; moreover, the various studies of one-half and other partial embryos had raised new problems. It was no longer necessary to argue for the value of studying embryology. And embryology did not bring with it all the old assumptions of the morphological tradition, for that tradition had itself evolved and developed. As E. B. Wilson wrote in his 1893 lecture, the last ten years had brought a "remarkable awakening of interest and change of opinion" in embryology, especially about the significance of cell cleavage. In this major lecture, Wilson moved beyond the traditional program in morphology to new concerns, though those remained essentially morphological.[64]

In that essay, Wilson rejected the germ layer theory which had dominated embryology, arguing that one must begin with cells to trace cell lineages rather than begin with germ layers. As discussed earlier, Wilson looked favorably on an epigenetic view of development and rejected the Weismann–Roux mosaic theory. He urged that though biologists were "still profoundly ignorant of the nature and causes of differentiation, and of its precise relation to cell-formation," that nonetheless it had become clear in the preceding few years that differentiation often coincides with cell boundaries and hence was "not entirely independent" of cell formation.[65] Careful study of cleavage, of fertilization, of all the early developmental changes in cells and their relations to differentiation appearing

64. Discussed in detail by Alice Levine Baxter, "Edmund Beecher Wilson and the Problem of Development: From the Germ Layer Theory to the Chromosome Theory of Inheritance," Ph.D. diss., Yale University, 1974; Baxter, "E. B. Wilson's 'Destruction' of the Germ-Layer Theory," *Isis* 68 (1977): 363–374.

65. Edmund Beecher Wilson, "The Mosaic Theory of Development," 1893, p. 14.

later were indicated as a priority for biology—all assuming that the cell was a, if not the, fundamental unit of development and heredity.

Several other papers in 1893 and later addressed precisely such phenomena. "Fertilization of the Ovum" by Edwin Grant Conklin (1863–1952) examined the relative roles of nucleus and cytoplasm for development and concluded that "the *entire* cell is still the ultimate independent unit of organic structure and function." Though the vast majority of biologists were coming to endorse the nucleus as the bearer of heredity, Conklin insisted that both nucleus and cytoplasm played crucial roles in both heredity and development. After all, fertilization brings together parts of both male and female cytoplasm as well as nucleus; for example, the sperm aster is cytoplasmic. The "independent unit of structure is still the entire cell, not cytoplasm alone, nor nucleus alone, but the two together," he maintained.[66] This unified, coordinated cell is where embryologists should begin their study of the patterns and causes of differentiation.

Watase agreed, also in 1893, that morphologists were explaining origin and development in terms of cell growth, and physiology in terms of component cells. The cell may well have arisen by a symbiotic union of two units, becoming the cellular nucleus and cytoplasm. The symbiotic relations are adaptive so that now nucleus and cytoplasm need each other, with neither any longer capable of survival alone and with each keeping the other under control. Fertilization simply brings the synthetic product of one cell from two, and cell division is essentially incidental to increase in both nucleus and cytoplasm. Thus, the symbiotic cell retains a primary biological importance for Watase.

Yet Whitman objected to what he saw as "the inadequacy of the cell theory of development," which Conklin, Watase, and others accepted. Cells are important, of course; indeed, the organism is the product of cell formation. But above the cell, the whole organism predominates. We see a similar position expressed by Whitman's colleague at the University of Chicago, Charles Manning Child (1869–1954), in his 1899 lecture. "It is the *organism—the individual, which is the unit and not the cell,*" Child emphasized.[67] Cells act together, as a unit, because of the organization of the whole. Differentiation and formation of the organism are not due to cell

66. Edwin Grant Conklin, "The Fertilization of the Ovum," 1893, pp. 34, 32.

67. Charles Manning Child, "The Significance of the Spiral Type of Cleavage and Its Relation to the Process of Differentation," 1899, p. 265.

division, to cleavage, or to some mysterious "cellular interaction," Whitman agreed with Child. For the claim that the egg already experiences definite organization, he believed he had decisive proof. All cell divisions do not simply divide up the differentiated areas already laid out but can cut across those areas. Whitman agreed with Huxley that cells are like sea shells; they are the effects that show where the tides, or developmental processes, have acted. They are only effects, so that cell division cannot be a cause of differentiation. Cell lineage, for Whitman, was valuable for demonstrating the patterns by which the whole functioning organism gained its organization. As Lillie wrote of Whitman after his death,

> Whitman took a strong and independent position, basing his conclusions not merely on comparative embryology but also upon the comparison of protozoa and metazoa. He protested against the view that organization is the product of cell formation, and insisted that "organization precedes cell formation and regulates it." He contrasted the Cell-doctrine with what might be called the Organism-doctrine. He insisted that, "an organism is an organism from the egg onward, quite independent of the number of cells present," and that cleavage is not a process by which organization arises, but that organization precedes cleavage."[68]

Despite his strong view, Whitman did not force his ideas on others. Though dogmatic about principle, one of his principles was to remain scientifically undogmatic and to support and encourage proper scientific research. Thus, he encouraged open discussion and investigation, even when he disagreed with the conclusion. As long as the investigation was well designed and the results solid, and as long as the conclusions were expressed so as to reveal the open questions or points of disagreement, he did not object.

Whitman supported Loeb, for example, even when Loeb argued for a strictly mechanical, epigenetic view of development which seemed to degrade the significance of heredity. Loeb rejected many of Whitman's conclusions, yet Whitman supported him at the University of Chicago and made efforts, eventually unsuccessful, with the administration there to

68. Whitman, "The Inadequacy of the Cell Theory of Development," 1893, p. 124; Lillie, "Whitman," p. xliv.

ensure Loeb's staying. Whitman also invited Loeb to the MBL to head the physiology program which he regarded as a neccesary complement for morphological work.[69] By 1894 Loeb had embarked on his physiological program for morphology, as he considered it. He sought to determine the causes, inevitably mechanical and chemical, of animal forms. With a series of experiments on artificial production of cellular or of nuclear division, he established features of the mechanics of growth and formation which emphasized physicochemical tropisms directing development. "Heredity" offers no explanation of that fundamental question, what causes the arrangement of the different germ regions, Loeb insisted. Thus, neither parental conditioins nor other evolutionary factors play any role. Instead, all phenomena are determined by chemical processes, with differences in energy amounts or resistance explaining differential growth. Physiological morphology will provide the laws of organization due to chemical activity of the cell. But it also has the synthetic goal of allowing man to form new combinations from nature. Control as well as analytical understanding was what Loeb sought.[70] Such a program would not have appealed to Whitman, or to most of the others at the MBL by 1894, but Whitman accepted Loeb's alternative "standpoint" as important for the cooperative idea of biology.

In a different way, we find tolerance of occasional lectures by botanists. After all, the MBL considered all of biology, in theory at least. Difficulties in obtaining a botanist with interests parallel to Whitman's and thus in integrating botany with zoology, and the less "sexy" nature of botanical work at the MBL contributed to botany's secondary status there as elsewhere in leading American biology programs.

1894 In two series of lectures, 1894 and 1898, Whitman encouraged consideration of the details and significance of cell division. The 1894 lectures he regarded as dealing "with one or another side of the problem of organic development—that problem which has led, and which will most likely ever continue to lead, the biological sciences."[71] Comparison of different standpoints could prove valuable to all sides. The published vol-

69. MBL *Annual Reports,* plus various items in the University of Chicago Archives in the Whitman Papers, Presidential Papers, and Zoology Department records.

70. Jacques Loeb, "On Some Facts and Principles of Physiological Morphology," 1893, pp. 37, 53; Loeb, *Untersuchungen zur physiologischen Morphologie der Thiere* (Würzburg: Hertz, 1891; 1892) I, Heteromorphosis. II. Organbildung und Wachsthum; Pauly, "Jacques Loeb."

71. Whitman, "Prefatory Note," 1894, pp. iii–ix.

ume began with several general lectures addressing problems of development, meaning ontogeny, heredity, and evolution, then focused more directly on cell action.

The Tufts University physicist Amos Emerson Dolbear (1837–1910) and John Ryder opened the series with theoretical examinations of heredity from a largely mechanistic, physicalist perspective. Then Osborn, in a lecture reprinted here, cited the need for using inductive approaches in biology, for rejecting excessive speculation, and for avoiding the "unnatural divorce" of specialties from their common goals. In particular, embryologists and paleontologists should work together to develop a theory of both these intimately related phenomena or their fields of study.

An essay by George Baur (1859–1898) also considered evolution, but more directly. In fact, his discussion of speciation in the Galapagos Islands represents a notable departure from most of the published lectures in the series. Though a number of oral presentations had considered such traditional evolutionary questions, very few appeared in the published papers. Born in Germany, Baur had served as an assistant at Yale, then went to Clark University in 1890, as Whitman had. After a visit to the Galapagos in 1891, Baur moved with Whitman to Chicago in 1892, as assistant professor of comparative osteology and paleontology. Whitman knew that Baur had put forth a theory, based on his own study of Galapagos species, which directly contradicted Darwin's and which had stimulated considerable controversy.[72] Presumably that explains Whitman's invitation to Baur to serve as instructor at the MBL in 1894 and to present an evening lecture. There, Baur expressed his view that the harmony of species distribution could only be explained if the islands had resulted from subsidence. Instead of the islands' having arisen from the ocean and having been populated by migration from the mainland as Darwin suggested had occurred, they were isolated by subsidence, or a rise of water level. Isolation produced speciation, he argued. Only that theory could explain the harmony evident among species on the different islands, Baur maintained even in the face of powerful opposition. As he began to gain supporters, his theories received considerable attention.

Returning to a more familiar theme of the published lectures, E. B. Wilson urged the value of embryology, and indeed of morphological embryology. The embryological method based on the biogenetic law, which assumed that embryological development (ontogeny) repeated the an-

72. William Morton Wheeler, "George Baur," *American Naturalist* 33 (1899): 15–30.

cestral history (phylogeny), had been basic to morphology. But both that embryological method and morphology urgently needed revision, since both had come to be regarded with distaste. "The truth is," Wilson admitted, "that the search after suggestive working hypotheses in embryological morphology had too often led to a wild speculation unworthy of the name of science." Nonetheless, embryology can be worthwhile, and even valuable, as a guide to homologies. Researchers needed a "trustworthy basis of interpretation," a candidate for which Wilson went on to suggest. Biologists should not abandon embryology altogether, nor the traditional descriptive and comparative accumulation of facts which are, after all, the "very framework of biological science." But avoiding speculative excesses does not also require a complete endorsement of experimental methods and rejection of more traditional methods. Embryology must use various methods and provide itself with a solid foundation, recognizing that "the greatest fault of embryology has been the tendency to explain any and every operation of development as merely the result of 'inheritance,' overlooking the vital point that every such operation must have some physiological meaning for the individual development, hard though it may be to discover."[73]

Turning directly to the significance of cell division in his essay, John McMurrich also acknowledged the recent remarkable developments in embryology, especially with cell lineage and physiological studies of the embryo. Researchers had also turned attention to the particular question of what determines the direction of cell cleavage. Because it proved difficult to discover adequate mechanical causes, the experimental physiologists had tended to look outside the cell itself, to external causes such as pressure and gravity. This led to apparent but possibly deceptive simplicity. Probably none of the extreme views would prove correct, McMurrich thought, in keeping with the MBL tendency to adopt intermediate positions.

Watase examined the origin of the centrosome, concluding that it came from cytoplasm and that the cytoplasm thus had a "certain endowment" not fully recognized. Since the centrosome seemed associated with protoplasmic movements, its role in directing cell division and cell action should prove important.

In 1894, then, Whitman had organized the series of lectures to attack questions about morphology and about the role of embryology with respect to heredity and evolution, and to raise considerations about the role

73. E. B. Wilson, "The Embryological Criterion of Homology," 1894, pp. 103–104, 123–124.

of the cell and cell division. These were all central issues of the day for biologists and were not particular pet problems of Whitman's. They all arose from the flurry of experimentation and interpretation pouring out of Germany, against the background of cell lineage and other morphological work carried on in the first years at the MBL. Wheeler's translation of the introduction to Wilhelm Roux's new *Archiv für Entwickelungsmechanik* illustrated the interest of Americans in—though not their acceptance of—the German work. That important essay reveals Roux's self-confident, indeed bombastic, style and his commitment to a mechanical and experimental program for embryology, which provided such a center of interest for MBL researchers.

1895 The year 1895 brought a move to consider general biological phenomena. The seemingly assorted set of papers actually represents a cross section of current, largely nondevelopmental concerns. Infection, immunity, Huxley, paleontology, descriptions of segmentation, bibliographic materials, transformation of plant parts: these represent biological subjects, broadly interpreted, and may well have reflected Whitman's attempt to remind the MBL audience that biologists should be concerned with more than development, heredity, and evolution. The papers by Dolbear and Watase bear particular interest in revealing those general concerns.

Dolbear presented a view of biological knowledge based on mechanical, chemical, and physical causes. Yet he, like Whitman, did not adopt a radical reductionist position, in which all life is regarded as explainable in terms of minute particles acting just as they would in any physical system. Such may be the actual basis of life, but life exhibits a level of complexity which may warrant explanation in terms of material units and their relations. Whitman suggested that, just as there is an organic chemistry, there might well be an organic physics, distinct not in kind but in complexity. A mechanist rather than a vitalist, Whitman nonetheless regarded life as calling for explanations falling short of extreme, radical mechanism. He embraced what might today be considered a form of emergentism. As Whitman had said in 1894:

> The search for ultimate units of organization in the egg—that is, smallest elements capable of organic growth and self-division—has already led directly to the discovery of *mechanism*, where molecular epigenetics had disputed it. The molecule is no doubt universal and very mighty, only perhaps not quite almighty. It is quite conceivable that there should be something at least as far

> above the molecule as the molecule is above the atom. Indeed, there seems to be a considerable number of units actually visible in the cell, which are certainly quite as real as the molecule, and which differ from it in having those fundamental attributes of growth and self-division which appear to be peculiar to every grade of organic life. Every such unit may be reducible by chemical disintegration to molecules, but we should hardly accept that as proof that no organization above molecules preceded the dissolution. There is no warrant for the assertion that life is something different from, and independent of, matter and energy. That is the mistake of vitalism. On the other hand, there is no warrant in decomposition for identifying dead mechanism with living mechanism.[74]

Whitman clearly found it important to assess the proper basis for biological study and the relation of biology to physics.

In the lecture series of 1894, Dolbear had discussed "Life from a Physical Standpoint." There he had stressed the necessity of hypotheses for guidance in science and had cited Darwin's theory of natural selection as the "only rational hypothesis" of the time concerning the "nature of life." The best hypothesis about the composition of organic nature was also that phenomena of life are resolvable into physical and chemical processes, so that life is an attribute of matter just as surely as electricity and gravitation are. Essentially, for Dolbear, life is the result of a field of activity resulting from a complex of vortex atoms in the ether, again just as gravitation, magnetism, electricity, or chemical attraction are. Yet he acknowledged that there could be something different for organic matter, though certainly not a vital force or vital entity. Dolbear's particular view of physically based life was very like Whitman's own, though worked out much more clearly and in terms of current ether and field physics of the 1890s.

Whitman invited Dolbear back for an additional series of five lectures in 1895, two of which he published. In the first, Dolbear denied that any such thing as a vital force exists; indeed, energy itself is a product of more basic changes. Thus, a proper explanation, in biology as elsewhere, "is complete when the physical and chemical antecedents have been presented in their order and quantitative relations." Life may be more complex than, but not fundamentally different from, nonlife. In his second lecture, Dolbear reiterated the essential chemical and physical nature of

74. Whitman, "Prefatory Note," p. vi.

living matter, then went on to deny any form of mind-body dualism. There simply is no evidence that mind exists separate from matter. Rather, consciousness results from nervous energy, itself a product of motion of ultimate particles of matter. Mind results just as magnetized iron results, due to rearrangement of molecules.[75]

Certainly not all biologists in the world would have agreed with such physicalist but not radically reductionist proclamations, but generally the American researchers, and especially those at the MBL, did. Even those sympathetic to Driesch's later turn toward philosophy and his rejection of the Weismann–Roux form of predeterminism and self-directed developmental mechanics did not embrace vitalism. Dolbear's clarifications and explicit statements undoubtedly helped many who had never really articulated their assumptions about the nature of the phenomena they investigated.

Following Dolbear's contributions came a lecture by Watase, this time explicitly examining the physical nature of a peculiar biological phenomenon. Animal phosphorescence might well seem like a peculiar living phenomenon, as indeed it had in the past. Yet, as Watase urged, we can know life only through its physical, chemical, and mechanical manifestations, of which the emission of light is one example. Light production is of no use to some insects but is of value to others. The ability to produce light has what might appear to be two causes, one proximate, the other ultimate: "While the production of light may be regarded as belonging to the same ultimate cause as that of heat, the proximate cause of the luminosity in the animal kingdom may be due to a variety of secondary circumstances."[76] In fact, it is the background or ultimate substructure which really explains the phenomenon. Chemically, production of light requires oxygen, hence respiration. Perhaps the oxygen combines with some dead substance prepared by the cell normally and in some cases produces luminescence. This one phenomenon may well be connected closely with the "whole mystery of life."[77] With Watase's lecture, then, we see a particular biological application of Dolbear's and Whitman's general viewpoint concerning the chemical and mechanical nature of life.

Paleontology is a morphological discipline, asserted William Berryman Scott (1858–1947) in his lecture. Paleontology considers "the factors of

75. Amos Dolbear, "Explanations, or How Phenomena Are Interpreted," 1895, p. 73; Dolbear, "Known Relations between Mind and Matter," 1895, p. 93.

76. Shosaburo Watase, "On the Physical Basis of Animal Phosphorescence," 1895, pp. 107, 113.

77. Ibid., p. 118.

evolution, the causes which determine the development of new forms, and the problems of heredity which are inseparably connected with them." Ultimately, the decisive evidence will probably come not from paleontology itself, however, but from "the physiological and experimental method," meaning experimental embryology. Indeed, "experimental embryology has already won some notable triumphs, and that is a physiological quite as much as a morphological province."[78] Cooperation of different disciplines and of different approaches will prove the only way to cut through the vast accumulation of facts to answer the pressing questions, Scott concluded, echoing a favorite theme at the MBL.

1896–1897 A selection of the lectures from both 1896 and 1897 appeared together as the fifth volume of the series, perhaps partly because of Whitman's struggles with the Trustees over finances in 1897 and the resulting near failure of the MBL to open at all that year.[79] Again, we find a mixed set covering the range of topics that Whitman regarded as properly biological. Lectures on the sparrow, on paleontological methods, excretion, neural terms, plant classification, and biological stations represent the range of topics. All address subjects of general interest and tie the discussion in with broad concerns. Four of the essays focus more directly on cell actions in development; amplifying a favorite theme at the MBL.

Conklin expressed the most widespread sentiment at the MBL with his emphasis on embryological questions: "Philosophically, the most important problems of biology are those which concern the origin of a new individual, the genesis of a living organism . . . The mystery which hangs about the process of progressive and coordinated differentiation by which the egg cell is transformed into the adult never loses its charm nor ceases to be a mystery." His insistence on the value of both observation and experimentation for embryological work, in opposition to Roux's demand for experimentation alone, also reflects an attitude typical of MBL scientists. As Conklin stressed, "There is no such sharp distinction between observation and experimentation in biology as is sometimes assumed; neither method can arrogate to itself a monopoly of certitude regarding facts or causes."[80]

78. MBL *Annual Reports* (1897); discussed in Lillie's history of MBL in a number of places and in letters of Whitman to Conklin, Lillie, Wilson, and Morgan, MBL Archives.

79. William Berryman Scott, "Paleontology as a Morphological Discipline," 1895, pp. 58, 60.

80. Edwin Grant Conklin, "Cleavage and Differentiation," 1896–1897, pp. 17–18.

Evidence was accumulating, Conklin said, that something like Wilhelm His's organ-forming germ regions might in fact exist. Assuming they do, that the egg is thus already organized to some degree, then what significance does cell division have for differentiation of the organism, that "most important problem of biology?" Cleavage may logically either (1) follow the pre-established regions; (2) cut across those regions; or (3) merely chop up homogeneous material (if one rejects His's organ-forming germ regions). The first of these Roux captured with his mosaic theory; the second was Whitman's "organization theory"; while the third was the "homogeneity theory" endorsed by Driesch and other extreme epigenetic physiologists. In fact what happens, Conklin asserted, is that all three pertain, but for different organisms. Some, such as annelids and gastropods, have a very regular, determinate, or mosaic, cleavage. Echinoderms, vertebrates, and others generally experience indeterminate cleavage, whether explained by (2) or (3). Experimental production of whole embryos from half the material does *not* support the contentions of Driesch in particular, that the egg material never had any organization, that cleavage was thus proven indeterminate. Rather, the artificial experimental case showed nothing more about normal development than did regeneration studies. Normal development might proceed in a highly constant and determinate manner, but disruption might bring other factors into play and produce necessarily adjusted and hence indeterminate cleavage.

Determinate cleavage under normal conditions results not from chance nor from extrinsic mechanical factors, which direct indeterminate cleavage. Rather, the cause must lie with the protoplasmic structure of the cells. Constancy of the first cleavage indicates constant protoplasmic arrangements in the unsegmented egg, or intrinsic factors. All of these intrinsic factors depend on the organism's history, for "the reason that a certain blastomere arises in a certain way, passes through a definite developmental history, and in the end gives rise to a definite part is at bottom the same reason that the egg of a given animal passes through a definite history and gives rise to a definite organism."[81] Similarities, or constant mosaic cleavages, generally predominate in the earliest stages, while divergence of cell division and differentiation increase as development progresses. Conklin's distinctions and clarifications became a standard, even for those who disagreed with his conclusions, for subsequent discussion of cell cleavage.

81. Ibid., p. 34.

This essay also serves to invalidate the incorrect impression that some modern researchers have of the work at the MBL. J. M. W. Slack wrote recently in a review of William Jeffrey's and Rudolf Raff's edited volume of MBL lectures from 1983, that

> ever since the days of Whitman, Wilson, and Conklin, Woods Hole embryologists have been of the school that believes that regional specification arises from the passive partition by the cleavage planes of regulatory molecules differentially localized within the egg. Such mechanisms do indeed operate in some cases, and the second half of the book includes much of the best evidence. However, it seems to me that in all these cases the localization only represents the *first* decision and that all the remaining pattern of the embryo becomes specified as a result of interactions between the parts.[82]

Conklin, Whitman, and Wilson would surely have agreed. Such a statement fails to recognize the sophistication of the MBL work of the 1890s and the understanding by the principals that many features, indeed more than Slack might well admit, *do* work together to effect embryonic development.

Katherine Foot (1852–1944?) presented the first of two lectures at the MBL given by women. Her consideration of the origin and function of the centrosome in development follows the standards of the time. She concluded that two centrosomes exist, one from each parent, and that both are cytoplasmic rather than nuclear elements. Also typical of the time, she presented her conclusions as preliminary, as the best available hypothesis, to be revised in the face of new data and new ideas. Whether because of her own reportedly somewhat negative personality, or because of feelings of insecurity in her role as first woman lecturer, or because of an exaggerated sense of honesty, she concluded, excessively apologetically, that "I believe I really *know* very little about the subject, and when I have read more I shall probably know less."[83]

Henry Crampton's (1875–1956) lecture on coalescence experiments extends Gustav Born's (1851–1900) transplantation and grafting experiments to the Lepidoptera. Just as Conklin and Albert Davis Mead (1869–1946)

82. J. M. W. Slack, review of William Jeffrey and Rudolf Raff, eds., *Time, Space, and Pattern in Embryonic Development*, in *American Scientist* 73 (1985): 293–294.

83. Katherine Foot, "The Centrosomes of the Fertilized Egg of Allolobophora Foetida," 1896–1897, p. 57.

considered cell division as "close to" the most fundamental of biological problems, Crampton regarded animal grafting and resulting coalescence or tissue hybridization as "among the most important."[84] He hoped to gain further information about the role of heredity in producing color by grafting together pieces of differently colored species. Did the gonad and color have a common cause or did the gonad (and hence heredity) cause color? He succeeded in grafting together pieces of tissue, notably fronts and backs of different individuals. Unfortunately, the results concerning color production remained inconclusive, and he could not answer his own question.

Whitman evidently acknowledged the grafting techniques and possible results as valuable for embryological research. He tried on several occasions to persuade Ross Granville Harrison (1870–1959), a Trustee who spent some time at the MBL during several summers and who was a close friend of several regulars there, including Conklin and Morgan, to discuss his transplantation work in frog embryos. Not one to enjoy giving public lectures, Harrison came close to agreeing but never actually presented a lecture at the MBL.[85]

1898 A series of coordinated and largely embryological lectures came in 1898, the year after Whitman's major battles with the Trustees. He still hoped to gain a permanent endowment for the lab and thus to make it an independent, national biological center with a secure financial base. To that end, he still sought publicity where he could find it. The *Biological Lectures* had proven successful in gaining wide and positive attention.[86] Perhaps he hoped that a series of lectures by his leading regular researchers and several students from Chicago on a topic of central importance in American work would exhibit the advances made by Americans and would reveal a productive program of research. Thus, most of the lectures focus on factors in differentiation. Two lectures on evolution by MBL regulars, former assistant director of the MBL Herman Carey Bumpus (1862–1943) and the paleontologist Scott, filled out the traditional topics. In addition, 1898 witnessed the introduction of Whitman's work on animal behavior, which had come to dominate his own research interests even while he still guided his students into studies of cell lineage

84. Henry Crampton, "Coalescence Experiments upon the Lepidoptera," 1896–1897, p. 219.

85. Ross Granville Harrison Collection, Yale University Manuscripts and Archives, and Whitman Collection, MBL Archives.

86. Whitman, "Prefatory Note," p. iii.

and differentiation. W. W. Norman's paper on pain illustrates a similar concern.

E. B. Wilson's two papers are both classics, revealing his clear thinking and solid morphological viewpoint, stimulated by his work at John Hopkins under Brooks and at the MBL with Whitman. These papers, together with his earlier contributions, nicely summarize his general assumptions in biology. The first acknowledges that the promise that knowledge of structure could provide sufficient information to understand the physiology of development was fading. That hope "is giving way to a conviction that the way to progress lies rather in an appeal to the ultra-microscopical protoplasmic organization and to the chemical processes through which this is expressed. Nevertheless, it is of very great importance to arrive at definite conclusions regarding the visible morphology of protoplasm."[87] As Darwin had suggested, protoplasm consists of heterogeneous corpuscles, an intricate network of different substances. Darwin's hypothesis of pangenes will not likely prove correct, nor are we likely to find a perfect alternative to account for physiological changes since the protoplasm is extremely complex. The structures we see are probably secondary, with finer and finer structures in the background so that eventually we reach what appears to be a homogeneous substance in which the structure remains invisible.[88]

Understanding the protoplasm is necessary but not likely to be fully realized: that dilemma ultimately contributed to the move by Wilson and others away from the research emphasis of the 1890s. They moved from cells and their morphological characters to different, more immediately productive research ventures, notably in cytology of the chromosomes and genetics.

Wilson's second paper is at first sight a throwback to his earlier cell lineage studies of 1891–1892. Then he had worked on the cell lineage of *Nereis* and discovered that Conklin, then at the United States Fish Commission at the Johns Hopkins table, was undertaking a similar "cell-counting" study of the gastropod *Crepidula*. Wilson walked over to meet Conklin; the two discovered striking similarities in the manner of development of their two forms. Wilson introduced Conklin to Whitman, who offered to publish Conklin's results in his *Journal of Morphology* and also thereafter introduced more and more students to cell lineage work. The

87. E. B. Wilson, "The Structure of Protoplasm," 1898, p. 2.
88. Ibid., pp. 15–16.

ideal of a group of individuals specializing on different organisms, then working cooperatively to arrive at generalizations by comparing their results and interpretations, obviously appealed to Whitman.[89]

Lillie recalled in his unpublished informal autobiography his first introduction to Whitman after he had determined to attended Clark University in order to work with Whitman. Whitman promptly encouraged Lillie to spend the summer at Woods Hole, and there set him to work tracing the cell lineage of the freshwater oyster *Unio*. This meant that Lillie had to trek back and forth by train from Woods Hole to a pond in Falmouth, lugging his collecting materials with him.[90] In the early years of the MBL, Whitman and his students and associates took cell lineage seriously.

Wilson's second paper of 1898 serves as an apology for that work at a time when the lure of experimentation and physiological questions had become strong if not irresistible. Cell lineage work and the embryological and evolutionary questions it illuminated remain at the core of biology, Wilson maintained. Every individual presents us with two problems together, he suggested. While it is a complicated mechanism in itself, maintaining a complex adaptive equilibrium of its own parts and with its environment, each individual also represents an adaptive product of past conditions. The physiologist or morphologist therefore has two tasks, the second including the study of that historical background. Cell lineage provides a new embryological method but provides no "open sesame" of perfect answers. Yet the suggestions and definite results are useful to demonstrate probable ancestral conditions. Unquestionably, ancestral reminiscences occur in even the earliest developmental stages and they serve as guides to genetic affinities just as they raise suggestive questions in pure morphology.[91]

Lillie followed Wilson with a general summary of the significance of his work on *Unio*, for cleavage in particular. Cleavage, when determinate as it is in *Unio*, reveals definite adaptations, results of internal conditions. Perhaps not the direct product of organization of the egg, the cleavage nonetheless follows some definite orientation or intercellular processes. Cell lineage work reveals the patterns of cleavage and exhibits a strong deter-

89. See Jane Maienschein, "Cell Lineage, Ancestral Reminiscence, and the Biogenetic Law," *Journal of the History of Biology* 11 (1978): 129–158.
90. Frank Rattray Lillie, "Autobiography," section 6, unpublished manuscript, MBL Archives, pp. 27–28; Lillie, "The Embryology of Unionadae," *Journal of Morphology* 10 (1895): 1–100.
91. E. B. Wilson, "Cell-Lineage and Ancestral Reminiscence," 1898, pp. 24, 40.

minate character, unchanged by the external factors which some had argued were alone decisive.

Conklin looked at the causes of differentiation, also illuminated by cell lineage work since he regarded the most important phenomena of development as those earliest stages: the development of polarity in the egg, for example. The causes are said to be due to the protoplasmic structure of the germ, but that means little without knowledge of the intermediate steps, he argued. This weakness of any hereditarian program, including genetics, continued to disturb Conklin, the committed epigenesist. Egg division and processes such as maturation, fertilization, and cleavage seemed the product of mechanical movements, perhaps vortex movements of the protoplasm. Here as elsewhere "the cell acts as a whole, and in the interaction of its various parts are to be found the causes of all vital phenomena."[92] Though he had not established the causes of the intermediate steps between egg origin and fully formed and differentiated individual, he was convinced that careful descriptive study of the protoplasm would reveal changes at least contributing to an explanation of cell division. Like Wilson and Lillie, Conklin reaffirmed the value of the morphological study of early cell actions. Also like Wilson and Lillie, he recognized that such changes reflect adaptations to past as well as present and later developmental conditions. Whitman's students Aaron Louis Treadwell (1866–1947) and Albert Davis Mead pursued similar lines of research and reasoning.

Cornelia Clapp's paper focused once again on the significance of the first cleavage plane. Instead of asking whether it resulted in a regular and definite way or whether it cut across differentiated regions, however, she looked to a slightly later stage of development. She asked whether the first cleavage plane decides the direction of the embryonic axis, as Roux and Eduard Pflüger (1829–1910) insisted, or whether that axis is already set in the egg, or whether the axis becomes established later. Whitman had encouraged Clapp to pursue her own research and had suggested that she examine the toadfish *Batrachus*, which has an adhesive disk to hold it in a fixed position. This unusual feature proved extremely valuable in allowing her to rotate the dish to which the egg attached itself and to test the resulting changes. Her preliminary results, published earlier, had demonstrated that the first cleavage plane and the embryonic axis coincided in only three of twenty-three cases, suggesting that some fac-

92. E. G. Conklin, "Protoplasmic Movement as a Factor of Differentiation," 1898, p. 90.

tor other than cleavage set the axis. Roux and Pflüger had challenged those results, with the effect that Clapp redoubled her efforts to establish her point.

In fact, she retorted, their work with frogs required fixing and marking procedures "which must always cast some doubt on the reliability of the results."[93] Her studies showed without question that the first cleavage does not coincide with the axis. The axis appeared in different cases in all directions from the first cleavage, a fact that she established with unfailing logic and clear evidence. Thus, "the study of cleavage has not yet given us any such fundamental laws of development as the mosaic theory claims." And "the opinion is gaining ground that the phenomena of cleavage are to be regarded as the expression of non-differential rather than qualitative divisions of the germinal material."[94] In thus challenging the strongly stated conclusions of Roux and his compatriots, Clapp had full support of the program in cell lineage and other careful descriptive and comparative morphological work encouraged by Whitman at the MBL. The physiological studies of Loeb and others, which emphasized the importance of physiological regulative responses to external conditions, also lent credibility to Clapp's attack on the simplicity of Roux's mechanically self-differentiating system.

Ironically, just as the set of lectures of 1898 summarizing the value of cell lineage work and the way in which heredity worked (for Loeb) and physical conditions shape development in regeneration (for Morgan) were delivered—and just as the group had come more closely together then it had previously in its series of summer lectures—Whitman turned his attention elsewhere. He had become attacted to a different set of biological problems altogether, to animal behavior. In some ways, his work signaled the coming of greater specialization and the loss of that ideal union. It also signaled the beginning of Whitman's withdrawal from MBL research and administration. But it represents Whitman's best work, and for that reason the paper of 1898 is reprinted here.

Psychogenesis, or the study of the emergence of habits, instincts, and intelligence, was as much a problem of natural history as Whitman's earlier work had been. Instinct, like development, resulted from adaptations chosen by natural selection. Indifferent organic material serves as a foun-

93. Cornelia Clapp, "Relation of the Axis of the Embryo to the First Cleavage Plane," 1898, p. 144.
94. Ibid., p. 151.

dation, from which gradual modifications bring instinct, then intelligence. "The adaptation of acts to purposeful ends must not be accepted too quickly as proof of intelligence in the doer," for adaptation may result from slow and blind selection among alternatives. From the leech *Clepsine* to his pigeons, Whitman examined details of behavior and suggested how they can be seen as results of selection and not of prior intelligence by the possessor. Choice comes when increased plasticity invites greater interaction of stimuli and hence facilitates conflicting alternative impulses. Education and learning result. "Plasticity of instinct is not intelligence, but it is the open door through which the great educator, experience, comes in and works every wonder of intelligence."[95] Development of intelligence and learning, then, is like development of form in that the individual begins with something inherited and adapted to past conditions, then learns through experience to respond to present conditions.

After 1898 Whitman continued to spend his summers at the MBL, but he became increasingly less a part of the research there. Indeed, by 1898 Whitman had been deeply discouraged by the conflicts of the previous year and had begun to withdraw from the MBL, from the University of Chicago, and from leadership roles generally. Though always available as an advisor, he no longer stimulated students to undertake projects closely related to his own. Most of the leading MBL researchers, such as Wilson, Conklin, Loeb, and Morgan, continued along their own paths of research, pursuing problems which grew out of their interests of the 1890s. Whitman's work diverged from theirs, though it also followed along lines initially included as part of the broad morphological tradition. Instead of studying marine organisms or worrying about the nature of biological research laboratories or American biology in particular, he turned to his pigeons. He laboriously packed them and hauled them back and forth from Chicago to Woods Hole for a few summers of research.[96] But the sort of experimental work such as Loeb's and Morgan's which was gaining predominance at the MBL, work which promised definite and relatively quick

95. Whitman, "Animal Behavior," 1898, pp. 298, 336, 338.
96. Ishikawa, "Whitman," 1911, p. 18: "His pet pigeons were abundant in numbers. He told me that when he started on a trip to the east, he took the pets with him. Year after year, the number is multiplied and he experienced increasing trouble in the transportation of the pets. So he quitted to come to Woods Hole, assigning the directorship of the Marine Biological Laboratory to Professor Lillie."

results but often without full consideration of the evolutionary historical past, did not appeal to Whitman.

1899 The last series of lectures, in 1899, reflects Whitman's own evolving concerns and his estrangement from the experimental work of embryology and physiology. Lectures on evolution and behavior dominate that year's offerings, though papers by his University of Chicago colleagues Mathews and Child discussed more traditional problems, as did Morgan's second installment on regeneration and Loeb's on fertilization.

Morgan's and Loeb's lectures, reprinted here, both reflect a move away from evolution and heredity which was seen as taking place in physiological work throughout the 1890s. Morgan rejected Weismann's views as placing too much emphasis on phyletic history, as appealing to a "shadowy past" which explained nothing. Certainly heredity plays some role in passing old characters from old cells to new, directed by the chemical substance of the cells. But inheritance cannot explain all. Regeneration shows how the materials of the organism change throughout the whole protoplasm. Regeneration exhibits regulation by way of physiological responses, though the process is so complex that Morgan resisted offering a final theory. Despite his reluctance, he made clear that it is development and response to external conditions rather than internal inherited factors which direct regeneration.

Loeb similarly deemphasized evolutionary or historical factors in discussing fertilization. Artificial fertilization, effected by altered concentrations of salt water, initiates development which can continue to the pluteus stage. These unfertilized eggs have no male component, yet develop normally to that point, demonstrating that whatever the male contributes to heredity is not necessary to initiate development. Loeb thus concentrated on the mechanical and chemical actions, and on the resulting tropisms set up in organisms. In fact, he emphasized that he considered "the chief value of the experiments on artificial parthenogenesis to be the fact that they transfer the problem of fertilization from the realm of morphology into the realm of physical chemistry."[97]

Though these two lectures concerned development, they had each separated out one aspect of development, ignoring general concerns of heredity and evolution. They had specialized. The focus of the other lectures presented had shifted as well. The paper by Daniel Trembly MacDougal

97. Jacques Loeb, "On the Nature of the Process of Fertilization," 1899, p. 282.

(1865–1958) on temperature inversion remains an anomaly in the series. It focuses on environment and relatively little on the effects of the climatic conditions on individuals. The other essays on behavior, evolution, and methods all represent different concerns than the *Biological Lectures* had pursued before.

The lectures by Edward Thorndike (1874–1949) reflect Whitman's new central interests at that time as well as the successes of the MBL's neurobiology course. That course, entitled the "Neurological Seminar," was directed by Howard Ayers (1861–1933) during its three-year run, 1896–1899. Designed "for the benefit of investigators who were willing to report the results of unpublished researches on nerve-tissue, and to summarize and discuss the literature bearing on each problem thus reported," the course became what we would today consider as increasingly psychological in content. Many questions of behavior, of mind, of pain, of instinct emerged in that seminar, and several of the papers found their way into the evening lecture series and on into the *Biological Lectures*. Thorndike's discussion of instinct held the general interest in such a multiple role.[98] "Instincts," he wrote, "are the expressions of structures and functions of the nervous system," and they "are as real and as important for the biologist as are bones and blood vessels." In all essential respects, Thorndike seconded Whitman's conclusions. In his second published lecture considering *Paramecium* behavior, he reinforced another of Whitman's pet assumptions by stressing that organisms act as a whole, not as the substance of which they consist. Comparing lower with higher organisms may well bring understanding of seemingly complex processes, as Whitman also assumed.

Another essay on *Paramecium*, by Herbert Spencer Jennings (1868–1947), covered some of the same ground but emphasized the importance of responses to stimuli. Using simple unicellular organisms, the researcher can uncover facts about higher processes as well. Thus, the apparent psychic powers of *Paramecium caudatum* dissolve into expressions of positive chemotaxis, Jennings concluded. Thereby "a long step is taken toward that analysis of vital processes into simple chemical and physical ones, which is deemed by many the final goal of biological science."[99]

98. MBL *Annual Reports* (1899–1903), p. 66.

99. Herbert Spencer Jennings, *Behavior of the Lower Organisms* (Bloomington: Indiana University Press, 1962); original 1906; Philip Pauly, "The Loeb-Jennings Debate and the Science of Animal Behavior," *Journal of the History of the Behavioral Sciences* (1981) 17: 504–515.

Jennings thus agreed with Loeb that biology should seek physico-chemical explanations, but by 1899 the two had begun to disagree about what that meant. Loeb emphasized internal tropisms, set up in the body as gradients of various physical and chemical factors. Jennings saw that some phenomena at least occurred more generally, elicited by various stimuli. Accordingly, he found the stimulus and response less specific. Though only suggested in his 1899 lecture, Jennings' conclusions were developed into a full-scale challenge of Loeb's theories by the time his book appeared in 1906. Though not an MBL regular visitor as most of the other lecturers were, Jennings clearly presented a point of view and offered experimental results directly centered on problems of interest to some of the MBL audience.

Charles Benedict Davenport (1866–1944) considered method in morphology in his lecture. Experimentation is nothing new for morphology and other studies, he pointed out, "but there has been a decided advance upon the methods in vogue a century ago." Notably, application of quantitative methods to zoology is an important addition. Do not fear that the step into the laboratory to count variations and establish frequencies will ruin the charm of biological work, he assured his audience, for one still must go out of doors to gather the specimens for study. Enthusiastic in his optimistic hopes for quantitative methods, Davenport suggested that "in the application of combined experimental and statistical methods to genetic [that is, those concerned with genesis or development] problems, zoology will reach its highest development."[100] Though perhaps not all ears at the MBL remained deaf to Davenport's message, research did not make any significant move in the direction of quantitative study for at least another decade. Population studies or frequency comparisons never characterized much of the work done at the MBL, largely because the MBL emphasized invertebrate and marine work. The populations of interest to most biologists did not come from the sea and were not those roaming individual invertebrates which the MBL researchers found most interesting.

CONCLUSION

The Americans, it should be clear by now, saw a complex of related problems of heredity, individual development, and evolution, or group devel-

100. Charles Davenport, "The Aims of the Quantitative Study of Variation," 1899, pp. 267, 270, 272.

opment. They rejected what they regarded as the simplistic theories of Weismann, Roux, and others. Those theories did not fit well with all the evidence at hand, or they failed to explain important facts, the Americans thought. Solid observation, comparison, careful consideration of alternative hypotheses—these features characterized the bulk of the work at the MBL. Perhaps the fact that researchers with different viewpoints and different emphases came together each summer and shared ideas and results served as a corrective to extremism. Over and over we find one or another researcher stressing the necessity of avoiding extreme positions. We find conclusions that what happens is a combination of various factors rather than just one. Especially as the Americans presented public lectures to mixed audiences and worked together teaching courses, they were forced to communicate, to cooperate, to achieve something of that union of specialist laborers that Whitman envisioned.

The 1890s brought hopes for a unified, cooperative biological science. Whitman believed in such a biology which would go beyond morphology and physiology; beyond zoology and botany; beyond embryology, evolution, and heredity. The Marine Biological Laboratory was intended to produce such a cooperative result, to illustrate that biology was one science. In retrospect, the effort did not really succeed. Much of what is properly biological never received attention at the MBL. As the decade moved on, individual investigators began to diverge in their research emphases and increasingly to specialize. Biology never quite became one science. Yet the efforts to address questions of general concern, as revealed in the *Biological Lectures*, and the fact that some questions *were* of general concern, demonstrates that researchers at the MBL in the 1890s at least hoped for a unified biology, even if they recognized that they had not quite achieved it and even if some believed that they might not.

LIST OF BIOLOGICAL LECTURES

1890 (PUBLISHED IN 1890)

1. Charles Otis Whitman, "Specialization and Organization: Companion Principles of All Progress—The Most Important Need of American Biology," 1–26.
2. Charles Otis Whitman, "The Naturalist's Occupation: 1. General Survey. 2. A Special Problem," 27–52.
3. Edmund Beecher Wilson, "Some Problems of Annelid Morphology," 53–78.
4. John Playfair McMurrich, "The Gastraea Theory and Its Successors," 79–106.
5. Edward Gardiner Gardiner, "Weismann and Maupas on the Origin of Death," 107–129.
6. Henry Fairfield Osborn, "Evolution and Heredity," 130–141.
7. Thomas Hunt Morgan, "The Relationships of Sea-Spiders," 142–167.
8. Shosaburo Watase, "On Caryokinesis," 168–187.
9. Howard Ayers, "The Ear of Man: Its Past, Present, and Future," 188–230.
10. William Libbey, "The Study of Ocean Temperatures and Currents," 231–250.

1891 (UNPUBLISHED)

1. Howard Ayers, "The Morphology of the Ear."
2. Henry Herbert Donaldson, "Methods of Studying the Nervous System."
3. J. E. Humphrey, "The Morphology of the Saprolegniaceae."
4. Edward O. Jordan, "Biological Analysis of Water."
5. John Sterling Kingsley, "A Trip to the Bad Lands."