Physiology in the American Context

1850–1940

Edited by
Gerald L. Geison

AMERICAN PHYSIOLOGICAL SOCIETY
Bethesda, Maryland

VII

Physiology, Biology, and the Advent of Physiological Morphology

JANE MAIENSCHEIN

Through Johns Hopkins's membership in the Society of Friends (Quakers) physiology first became a part of biology in the United States. As it turned out, physiology was only rarely accepted as a central part of biology. Although examples of this alliance remain few, they are nonetheless important and it is the earliest examples from the late nineteenth century that I shall explore in this chapter.

Johns Hopkins fell in love with his cousin; however, in keeping with Quaker doctrine of the time, his local Friends' meeting refused to allow them to marry. Because Hopkins never wanted to marry anyone else, the fortune he accumulated had to find other beneficiaries. Eventually he decided to donate his substantial resources to establish a new research university for Baltimore, with a medical school and a teaching hospital. Setting up two boards of directors to develop the university and the hospital, respectively, Johns Hopkins left it to the board members to determine how best to realize these objectives.[1] Although Baltimore already had ten colleges in the 1870s, none had anything like the healthy endowment of Johns Hopkins' new enterprises. The trustees chose Daniel Coit Gilman as president and decided to establish the university in advance of the hospital and associated medical school. As Philip Pauly has shown, this decision provided an atmosphere more conducive to the development of biology than would probably have occurred if the medical program had been established first.[2] True, the awareness of a coming medical school exerted some influence on the biological work there, but biology was nonetheless afforded the opportunity to develop on its own for several years.

At first, President Gilman had promised to build a program in natural history along with the other sciences of the day, but he knew how to consult the right people for advice and how to shift his goals when a revision was indicated. Thus he traveled to Europe and discussed his plans for this unusual new American research university with Thomas Henry Huxley, among others. Huxley convinced Gilman to design a broadly conceived program in biology rather than in natural history alone, which had different, less modern, and less scientific connotations. Gilman followed Huxley's lead in more than one sense, while also reassuring skeptics and critics back home in the Baltimore

community that biology was not really something radically new or threatening, but merely a combination of old friends: natural history and physiology.[3]

Gilman was sufficiently persuaded by Huxley's views that he decided to build his own program at Hopkins along the lines of Huxley's laboratory in South Kensington, London. In particular, this meant to Gilman that the department should be divided between morphological and physiological work.[4] In his role as keynote speaker at the opening of the Johns Hopkins University in 1876, Huxley expressed his approval of Gilman's decision. Noting that the biology program was intended to introduce students to medicine as soon as the medical school opened, Huxley insisted that the medical student should "come to his medical studies with a comprehension of the great truths of morphology and physiology, with his hands trained to dissect and his eyes taught to see."[5] Huxley thought that his was an appropriate program for both biology and medical students.

Given Huxley's role in Gilman's decision, what better choice for first biology professor at Hopkins than Huxley's assistant Henry Newell Martin? Martin had received England's first D.Sci. degree in physiology at Cambridge University working with Michael Foster, so he represented physiology very nicely. Martin was also prepared to teach physiology as part of biology. Job prospects for physiologists in England did not seem terribly promising in 1875, so Martin considered the invitation with interest. Nevertheless, this offer from a new university in a foreign land raised concerns; in particular Martin worried that casting his lot in America meant forsaking scientific research, if not civilization itself. After lengthy negotiations over salary, title, and laboratory details, he did finally decide to join the original Hopkins faculty of six, all young and half of them British.[6]

At Hopkins, Martin set out to establish a program in biology, which meant that first he established a physiology laboratory to pursue his own research, begun under Foster, on the action of the mammalian heart. In addition, however, he taught courses in general biology and he and Gilman hired a second instructor for the biology program, William Keith Brooks. Initially appointed as a postdoctoral fellow under Hopkins' generous and innovative fellowship program, Brooks had already received a promotion to assistant professor by the time he began his work in Baltimore.[7] Martin insisted that Brooks should not serve as his assistant, but instead should represent the other, that is, morphological, side of biology. Martin also insisted that he needed an additional assistant in physiology and he soon obtained support to hire William Henry Howell, then a student in physiology at Hopkins. As Martin laid out in a lengthy memo to Gilman, the department should eventually include representatives of biology, comparative anatomy and zoology, physiology, human anatomy, botany, and a museum curator. Because of the central role planned for medicine at Hopkins, Martin held physiology as the first priority, with other developments to follow.[8] In setting up this colony of physiological work in a biology department, Martin had to improvise. He had stepped outside the traditional homes for physiology, such as they were in the late nineteenth century, and into a different setting with new constraints. Thus the way he set up the department and his own role provided the primary examples for later institutional leaders to emulate or reject.

Given this unusual setting for a physiological program within a more broadly conceived biology program, Charles Rosenberg's suggestion that historians might experiment with an ecological approach to research disciplines has particular appeal." I can imagine Martin and the other physiologists in American biological programs as loosely analogous to the Arizona salamanders that one of my colleagues studies. Salamanders exist in Arizona in ponds or lakes, some of which dry up in the arid climate. Within a given population, some of these salamanders may exhibit a distinct cannibalistic trait: they devour their own kind. My colleague, who examines what factors influence the proportion of cannibals in the population, finds that density of individuals as well as elements of the food supply are relevant. With salamanders the population may change as individuals wander away, for example, or as heavy rains wash part of the population away to another pond, thus changing the situation in several places at once. Some ponds have no cannibals; others have many.

What is the analogy here? Surely I do not mean to suggest that physiologists are cannibals. Rather, in both the academic and amphibian cases, we have a minority form occurring within a larger, more normal population. Like the salamanders, physiologists existed in pools or academic environments, some of which dried up or changed with time. The proportion of physiologists within an environment as well as the resource supply were both relevant features in shaping the physiologists' own development. Some pools became completely zoological, others physiological. I am interested here in those biological pools with coexisting physiologists and morphologists, and particularly in the earliest such pools in the late nineteenth century.

The situation remains complex, so that defining biology generally, and physiology within it, becomes a process of untangling and understanding relations. No research program that self-consciously identified itself as biology existed before 1876 in America. Since biology as such did not exist before the arrival of physiology at Hopkins, both biology and physiology evidently arrived there at the same time. We cannot, therefore, consider the move of physiologists into a preexisting biology but only the parallel development of both.

Overall, given the ultimate lack of success of general physiologists within biology, physiology would seem to have had very limited success in colonizing the larger domain of biology. Generally, physiologists did not often achieve a balance with morphologically oriented zoologists within biology. For the most part they migrated instead into other, usually medical, pools. There, "non-biological" physiologists, namely those without any biological training or perspective, generally proved more successful and absorbed whatever resources were available for physiologists. As a result physiology in America developed as a largely medical discipline with the exception of a few early biological efforts. My concern here is with these exceptional efforts, specifically at Hopkins, the Marine Biological Laboratory (MBL), and the University of Chicago. Only the Chicago school really established a tradition of biological work in physiology, but all three offered important possibilities in the 1890s.

JOHNS HOPKINS

To pursue the first part of this quasi-ecological study, let us return to Johns Hopkins and Henry Newell Martin. Martin did set up a laboratory and pursued

some work of his own, especially studies of the mammalian heartbeat. In particular, he and his student collaborators isolated the heart and sustained its beating, then tested the effects of artificially (or experimentally) altering such conditions as temperature, arterial pressure, or ethyl alcohol concentration. Other studies examined the effects of respiration on the heartbeat.[11] A few advanced students climbed the stairs or ascended in the elevator to begin their own research careers in that small physiological laboratory at Hopkins, complete with its kymograph and characteristic smell. By 1887, in fact, Martin had produced nine Ph.D.s in physiology, at least seven of whom had continued to work in some aspect of physiological research—namely, Henry Sewall, Henry Gustav Beyer, Henry Herbert Donaldson, E. A. Hartwell, William Henry Howell, George Theophilus Kemp, Frederic Schiller Lee, William Thompson Sedgwick, and C. Sihler.[12]

These Hopkins men were trained as physiologists; in what sense were they also biologists, that is, in what sense did their institutional environment make a difference and thus reward us for pursuing an ecological approach to their history? All of them, though nominally students in biology, had received their specialized degree in physiology rather than the more general field. Indeed, at least as late as the 1890s, Johns Hopkins had awarded no degrees in biology as such, despite the label and the coexistence of course offerings in both physiology and morphology.[13] The physiologists in question did indeed take courses in morphology, meaning essentially comparative anatomy and embryology, with Martin's colleague Brooks. They were also eligible to join the summer sessions at the Chesapeake Zoological Laboratory directed by Brooks and designed to provide practical field experience in marine biology. Some actually did attend.[14] There they learned to think about the structure, function, and behavior of the whole organism. They also explored evolutionary relationships among organisms, as they would not in studying traditional physiology alone. A few of those Hopkins physiologists, including Lee, worked in biology before moving into the discipline of physiology per se. In a lecture before the biology section of the New York Academy of Sciences, Lee acknowledged that most people did not understand what physiology was and emphasized that physiology in fact went far beyond the medical study of humans.[15] At this point in his career, at least, Lee regarded the type of work he did as different from that of "biologists" in general, just as it was more than exclusively human physiology. Presumably his conviction was a result of the particular training he had undergone.[16]

No doubt individuals entered the Hopkins program and specialized in biological physiology for a variety of reasons. Those few who eventually earned Ph.D.s gained an unusual sense of what physiology could be and the plausibility of its role within biology broadly conceived. Yet nearly all migrated off to enter medical schools rather than to positions in zoology or in other fields of American biology. With the exception of Sedgwick's unusual position teaching biology and bacteriology at MIT, and Donaldson's appointment within biology in neurology at the University of Chicago, these Hopkins Ph.D.s did not receive offers from biology programs.[17]

Whereas before 1893 graduate students specializing in physiology had some opportunity to enter biology as a profession, after 1893 they did not. By then

Martin had himself largely withdrawn from his research, which had never been prolific anyway, so he could not help his students.[18] Martin's assistant, Howell, left Johns Hopkins in 1889 for the University of Michigan, there replacing his fellow Hopkins graduate Sewall, who had moved on to teach physiology in Denver. In 1892 Howell moved to Harvard, and then returned to Hopkins (after Martin's retirement and the simultaneous opening of the medical school) to assume the chair in physiology.[19] During the intervening years, physiology hit a low point at Hopkins, enough so that by 1893 Howell expressed his dismay at Hopkins' loss of prestige. Whereas "the Hopkins has been recognized as the one place in the country where graduate work in animal physiology was encouraged," Howell now lamented that the failure to appoint assistants had seriously undercut that former position.[20] After 1893, physiologists at Hopkins experienced increasing subservience to the medical goals of William Henry Welch and the general Hopkins medical ambitions.

The density of physiologists in biology in general also dropped in the late 1880s and 1890s so that a larger number of students in biology sought degrees in morphological work or zoology rather than in physiology. Individual factors including Martin's collapse from alcoholism also undercut physiological participation in biology and pushed students and researchers into the larger medical environment. True, a few new biology programs in the United States did embrace physiology, but not always of the Hopkins sort, while older programs did not rush to add physiologists at all.[21] In the late 1880s and early 1890s, "biological" physiology (as opposed to "medical" physiology) found a friendly environment only at Clark University, the University of Chicago, or the MBL, all of which centered around one man: Charles Otis Whitman.

CHARLES OTIS WHITMAN AND THE MARINE BIOLOGICAL LABORATORY

Charles Otis Whitman (1842–1910) played an intriguing role in the history of American biology. Although repeatedly only second choice for the jobs he held, Whitman used all his opportunities brilliantly. After attending Louis Agassiz's Penikese Island (Massachusetts) experiment in 1873 and again in 1874, he traveled to Europe for a Ph.D. under Rudolf Leuckart. Thereafter he applied for a fellowship at Johns Hopkins, but instead accepted an offer to teach zoology at the Imperial University of Tokyo, an opportunity that allowed him to begin crystallizing his ideas about how to train research scientists. In fact his four Tokyo students all became professional biologists, a remarkable record. Upon returning to the United States and after two years at Harvard with Alexander Agassiz, Whitman went to Milwaukee in 1886 to direct the Lake Laboratory for Edward Phelps Allis.[22] Once again recommended with several other people and not the clear-cut first choice, Whitman seized the opportunity offered in Milwaukee. His mandate there was to train Allis as a biologist and to develop a research station for morphological work. He also persuaded Allis to finance a new journal for American zoology, the *Journal of Morphology*, which began publication in 1887. Whitman insisted that Americans should not have to send their papers to Europe all the time and he convinced Allis and others of this point fairly easily.[23] If his position at

Milwaukee was less than ideal, he nonetheless used it well to make contacts, to bring other good researchers into the community (including William Patten, Howard Ayers, and Henry van Peters Wilson, as well as William Morton Wheeler, indirectly), and to continue his own research and articulation of his views about how biology should be carried out.

At one point Whitman applied for a job at Columbia, which he did not receive.[24] He had more success with other positions elsewhere, if only as the ultimately successful second choice. In 1888, for example, the Boston-based trustees of the MBL in Woods Hole, Massachusetts, offered Hopkins morphologist Brooks the post as first director of their new research and teaching laboratory. When Brooks declined the offer, Whitman accepted.[25] The next year, in 1889, Whitman received an offer to head the new program in biology at Clark University. Once again, Brooks had been offered the position first but had elected to remain in Baltimore,[26] and once again Whitman accepted and thereby joined the first string of influential leaders who defined the boundaries of American biology.

Whitman exhibited a continuing concern to articulate what biology is and should be. His convictions evolved gradually, partly in response to his changing institutional ties, as Pauly has argued. Indeed, Pauly interprets Whitman's statement of 1887 about biological instruction as an obvious job advertisement.[27] Perhaps this is so. Whitman originally presented the paper at a meeting of the American Society of Naturalists at a time when the various overlapping American biological societies (or incipient societies not yet formalized) were considering their respective roles. Whitman's interest in several of those societies may thus have stimulated his expression of what biological instruction should be like. Whatever its purpose, Whitman's paper advocated what he saw as a traditional German model for biological education, focusing on research as its chief end. A modern university should provide work in all the biological fields, he urged, ideally with separate institutes on the German model. Accordingly, botany, zoology, physiology, anatomy, and pathology should receive attention.[28] In Whitman's view, zoology included anatomy, histology, embryology, phylogeny, taxonomy, and physiology, with cytology as a more recent addition. These specialties were nothing to fear. Whitman reassured the American Society of Naturalists, but rather represented a necessary move in modern biological work. Zoology and botany remained the familiar primary divisions. In his role at the Allis Lake Laboratory in Milwaukee, Whitman had not yet been in a position to exploit those basic divisions in any practical way, yet he had clearly thought about how biology should be organized and taught.

In his first position of real national influence, at the MBL, Whitman had little chance to do much organizational work at first. Only seventeen people attended that first year, 1888; Whitman had only received his own invitation to assume the directorship in mid-May for the session opening on 17 July; and the announcements had appeared rather later as well. The first year's program at the MBL was thus limited and the atmosphere quiet, a feature that long-time investigator Cornelia Clapp recalled fondly in later more hectic years.[29] Whitman's second summer at the MBL brought more students and teachers, but followed a basically similar program, with one instructor to coordinate a

course of lectures for all the students. Whitman's report of that year urged the addition of a full-time instructor in botany and of two assistants to the chief instructor. Yet instruction at the MBL continued to proceed along the same lines as had Agassiz's school at Penikese, through a series of lectures on a wide variety of topics in biology presented by a diverse group of lecturers.

Not until 1890 did the MBL present more than one series of formal lectures. Courses in marine zoology, botany, and a special course on coelenterates were now offered by Whitman's colleague from Clark, John Playfair McMurrich. Undoubtedly, Whitman's move to Clark University as head of the biology program in 1889 led him to think more deeply about the relation between work in biology at the university and the summer laboratory. The move also allowed him to attract new colleagues to the MBL for lectures and research and thereby to widen the interests and offerings.

To this point, about 1890, Whitman had assigned physiology only a minor role at best and stressed morphological work instead, in accordance with his own training. For him, biology might well include a few physiologists, but they would remain relatively uninteresting in the general scheme of things. As Whitman assumed a role as director of several national programs, however, that attitude began to change. In 1890, he articulated more fully his view that biology must proceed with a division of labor among specialists who would then work together. Specialization was indeed desirable and necessary. Whitman announced in response to criticism that there was too much specialization.[30] Yet "Specialization is not science, but merely the method of science. For the sake of greater concentration of effort, we divide the labor; but this division of labor leads to interdependence among the laborers, and makes social coördination [sic] more and more essential. This is the law of progress throughout the social as well as the organic world."[31] After 1890 what may have begun as a rhetorical explanation of the particular selection of lectures for the evening series of public lectures given at the MBL became a persistent theme in Whitman's writings and letters, an ideal to which he became committed: the ideal of specialization and coordination working together.

At first Whitman's primary division of specialties for biology at the MBL included zoology and botany. By 1891, however, he had decided that he wanted physiology as a central part of biology. However, Whitman did not have in mind the traditional physiological work, which remained too closely allied with medicine and too narrowly centered on human studies. Instead he sought to promote a "biological physiology."[32] In particular he found recent work in the experimental physiology of development, such as that by Eduard Pflüger, Wilhelm Roux, Theodor Boveri, and others, of interest. He mentioned Jacques Loeb's ideas on "physiological morphology" as especially promising. Whitman reported that the limited resources available at the MBL had hitherto precluded the development of physiological work, but he clearly intended that the situation should change and he saw the physiology of marine organisms as particularly appropriate for his purposes. Accordingly, in 1892, Whitman added physiology to the MBL program, though not yet as a separate department of instruction or investigation, by inviting Loeb.

In his annual report for 1892, after Loeb had spent one summer at the MBL, Whitman focused on the relationships between physiology and mor-

phology. They were, he explained, two aspects of the same thing. Biologists pursue both morphological study and physiological study of adult organisms, developing individuals, and developing species. Morphology and physiology examine form and function respectively, and the two should come closer together. The physiologist must realize the significance of "non-adult" organisms or risk "having some of its most inviting fields pre-occupied and developed by morphologists." In particular, embryology should provide a meeting ground for both specialties 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."[33] Through work in the physiology of development Whitman saw the prospects for a true biological physiology.

He also saw the field as underdeveloped, suffering from "the lack of interest taken in general physiology, and the difficulty experienced in securing active coöperation [sic] from physiologists. As a rule physiologists look upon marine biology as something quite remote from their field of work, and the cases are rare indeed where they have taken an active part in seaside work."[34] Thus he regarded the MBL as fortunate to have attracted Loeb "whose enthusiasm, zeal, and accomplishments in general physiology, make him a fitting director of his department."[35] Several associates to help with instruction, including Lee, who had earned his Ph.D. in physiology under Martin at Hopkins, and a few students filled out the physiological program. Thus physiology first entered the MBL in 1892, with the formal addition of an instructional program in 1894 at Whitman's invitation and initially in the person of Loeb. The work evidently followed the lines of Loeb's research in physiological morphology, discussed next in more detail.

THE BIGGER PICTURE

To appreciate fully Whitman's commitment to introducing what he called biological physiology, or what Loeb called physiological morphology, we must understand the character of the MBL and the broader field of American biology a bit better. The MBL Board of Trustees began as a local Boston-based group, with several nonscientific members of the Woman's Education Association playing an influential role through their assistance in funding the MBL's predecessor under Alpheus Hyatt in Annisquam, Massachusetts. One of the trustees, Sedgwick, had been Martin's student in physiology at Hopkins and a fellow student of Edmund Beecher Wilson, who graduated from Hopkins in morphology. Wilson also became active at the MBL.

Wilson had played an active role in helping to direct the Chesapeake Zoological Laboratory under Brooks at Hopkins, had worked at the Naples Zoological Station, and had a strong commitment to marine biology. Because his teaching position in biology at Bryn Mawr from 1885 to 1891 left him relatively little research time and resources, he began to attend the summer sessions at the MBL, a habit that continued after he moved to Columbia in 1891 and for the rest of his life. E. B. Wilson's work on cell lineage fit closely

with Whitman's own embryological interests and made him an immediately attractive colleague, given the emerging MBL direction in both research and teaching. Whitman quickly saw Wilson as a kindred spirit, and by 1890 Wilson had become an MBL trustee and trusted advisor.

Meanwhile, when Wilson left Bryn Mawr for Columbia in 1891, he was succeeded at Bryn Mawr by another Hopkins graduate destined to assume a central role at the MBL, Thomas Hunt Morgan. In the same year, Loeb had let it be known that he wished to move from Germany to the United States. At the time, Whitman was settled at Clark University, Wilson at Columbia, and Morgan at Bryn Mawr. All of them knew of Loeb or his work and Whitman acknowledged him as a good biological physiologist. Pauly has suggested that both Whitman and Franklin Paine Mall, who was also then at Clark and had met Loeb in Naples, may have used their influence to secure Loeb a position at Bryn Mawr with the intention of transplanting him thereafter.[36] If so, the plan worked. Loeb moved to the United States to begin teaching and research in the biology program at Bryn Mawr in September of 1891. Here was a physiologist, trained in a medical environment in Germany and who had even practiced clinical ophthalmology (though not very happily), now in a biology program. If my analogy with the ecology of salamanders is useful, Loeb's move into the larger pools of biology on the American scene, initially if very briefly at Bryn Mawr, should have influenced both the character of his work and that of the surrounding population. There is some evidence that it did. Loeb's experience at Bryn Mawr helped to introduce him to American biological work and perhaps influenced or reinforced the particular kind of physiological work he pursued thereafter. Pauly reports that Loeb did not take gladly to the traditional embryological work that he was hired to teach at Bryn Mawr.[37] In fact Loeb found the preparation of sections and staining procedures tedious and deadly dull, an attitude that such embryological researchers as Ernest Everett Just later came to ridicule.[38] Loeb nonetheless reluctantly accepted his embryological tasks and thereby entered biology, as a general physiological morph amidst the dominant morphological and zoological forms.

WHITMAN AND CHICAGO

In 1892 the pools changed as something like a flood occurred. Biologists of all sorts were "washed away" from Clark University. Major battles with the administration at Clark led most of the biologists there (and indeed many of the scientific faculty members generally) to leave abruptly. They surely would not have migrated, some presumably to die, had no other pool with promising resources attracted them. The establishment, however, of another major research university, the University of Chicago, provided the desired new location. Mass migration from Clark to Chicago occurred, suddenly and generally, more like a flood than a purposeful migration.[39]

Whitman himself acted more carefully. After considering the advantages of making the move, he insisted that Chicago must provide an adequate modern laboratory for the biological sciences in order to make the move acceptable to him. Always interested in modern techniques and methods, Whitman consid-

ered the laboratory details crucial.[40] He had already given up on Clark, but he wanted to be absolutely certain that Chicago would prove more congenial, with a healthier supply of necessary resources to support a robust, diverse, and growing population. In fact Whitman had continually revised his ideas about what diverse specialties he wanted to have working cooperatively together under the broader rubric of "biology." Mall, convinced very early to move to Chicago, wanted Whitman to go as well. He thus worked hard to keep Chicago's President Harper positive about Whitman and to persuade Whitman that he needed Chicago and should not accept another offer he had evidently received.[41] Mall's efforts paid off, for Chicago and for Whitman, at least at first. Whitman finally allowed himself to be persuaded and accepted the call to Chicago in 1892.

In his early correspondence with Chicago's new president, William Rainey Harper, in 1891, Whitman outlined what he would want from Chicago—namely programs in zoology, botany, paleontology, and physiology, with anthropology to follow. He claimed that he already had with him at Clark one of the very best men in the country in paleontology and another in anthropology. He had others with him as well, professors and assistants. In a letter of March 1892, Whitman further expressed his desire that "Physiology, Anatomy, Histology, Embryology, Zoology, and Botany—should not fare worse than a science representing a much more limited domain."[42] He referred to chemistry, which had just received a substantial gift for its laboratories. This early correspondence between Whitman and Harper considers the biological sciences one department, presumably subdivided into specialty studies. Yet because Whitman kept referring to different specialties, he may well have confused President Harper about what he really sought for the biological sciences as Chicago.

In an undated memo, though it presumably reflects his ideas soon after arriving at Chicago in 1892, Whitman sought to clarify his views. There he referred to biology as divided into zoology and botany, with each in turn divided into morphology and physiology.[43] To reach European standards in that particular subset of biology that Whitman knew best, namely animal morphology, would require the development of several further subspecialty areas: zoology, anatomy, histology, neurology, paleontology, and pathology. Anthropology, cellular biology, and experimental biology would follow as further, more recent subspecialties. Within physiology, one finds human physiology, general physiology, physiological chemistry, and hygiene as the first subdivisions, with psychology coming later: Whitman regarded psychology as essentially physiological but as falling somewhere between physiology and neurology. Botany would consist of structural botany, physiological botany, systematic botany, and bacteriology. All botanical work, in the beginning at least, could exist together in the same organizational unit or institute, while the other subspecialties should each have their own units, following Whitman's perception of the structure of German universities.[44] He obviously knew most about zoological morphological study, about which he wrote in great detail, but Whitman's grand ambitions for biology did not stop there. He intended and probably fully expected to develop all branches, and he expected support from the administration.

Whitman thus went to Chicago with high hopes. He took most of the Clark faculty in biology with him, including Mall, Donaldson, George Baur, and Wheeler. He also attracted Loeb, as he had already done at the MBL, to develop the physiological side of biology, beginning that first year, 1892.[45] Despite Loeb's claim in a letter to a friend that he was surprised by the offer from Chicago, he had already written a letter to President Harper in June 1891 specifying his qualifications and explaining that he intended to make his home in America.[46] Having procured all this talent for Chicago, generally at lower salaries than he thought they actually deserved, Whitman felt he had the makings for the first-rate biology program he sought to establish.

President Harper and the University of Chicago, however, were not quite so forthcoming on all that they had promised or implied they would provide. The permanent laboratory buildings had to wait until after 1895, when Helen Culver gave $1 million for the development of the biological sciences at Chicago.[47] Whitman had to watch helplessly, though never patiently or quietly, as some of his leading researchers received better offers elsewhere that Harper could not, or would not, match.[48] The lack of proper funding for equipment was another persistent problem and the continued failure to establish an inland research station hampered research and caused Whitman and others great concern.[49] By 1899, Whitman had become deeply frustrated, as is clear from the following letter to President Harper written from Woods Hole:

> Within a few months zoology loses two men that are known throughout America and the whole scientific world as biologists of the first order. When such men go, everybody knows why they go, and they do not ask what is the matter with the man, but what is the matter with the University.
>
> P. S. Yours of August 30 at hand, I can make recommendations for the vacancies, but I would be glad to know first of all what can be done to put the department into working order. With no aquaria, no museum, and no laboratory service, and with appropriations cut to the lowest figure of a vegetative existence, it will not be easy to get such men as we have had. Nothing less than a thoroughgoing reorganization is possible or even worth doing.... So far as men are concerned we have had the best dept. in the country; so far as equipment is concerned we have had the *weakest* in nearly every respect. That has crippled us and led to dissatisfaction and steady decline. Your best help is needed. What do you propose?[50]

Perhaps all modern administrators will recognize the complaints and the resulting loss of morale that comes when great promises are broken and great hopes frustrated. Indeed, most of the men who had gone to Chicago with Whitman left for better situations, which disturbed Whitman personally as well as professionally. He especially lamented the loss of Shosaburo Watase, who he regarded as the very best cytologist of the day, better even than Wilson. Watase combined a physiological and a morphological approach to his work, as well as working with both plants and animals. He was therefore invaluable for the kind of program of cooperation that Whitman wished to build and it saddened him to lose Watase and others with similar talents, such as Wheeler.[51] Gradually, Whitman gave up and retreated into his work on the behavior and evolution of pigeons but only after continually fighting through the 1890s.[52]

In the end, Whitman's failure to achieve all the goals of his program can be

explained partly through his unrealistic demands and ambitions. His problems with the administrators at Chicago paralleled his relations with the MBL trustees; he had also wished to expand the MBL into a major research and teaching center while the trustees resented the increasing costs that seemed inevitably to come with such expansion.[53] In 1892, when Whitman announced to the MBL trustees that he was adding a course of instruction and investigation in physiology, headed by Loeb, he urged them to provide more funds to equip the physiology laboratory.[54] For the prior two years of his directorship, Whitman had disagreed with the trustees, who envisioned a slow development for their local laboratory while he saw prospects for a first-rate facility for research and teaching in the most up-to-date biological areas. Whitman at times took no salary from the MBL or spent what he did take on what he regarded as necessary laboratory expenses, just as he spent much of his salary at Chicago on establishing and maintaining a pigeon colony for his research on animal behavior.[55] Certainly Whitman demanded no less of himself than he did of others, including the administrators of both the MBL and Chicago. Yet they could hardly be expected to share his vision and singleness of purpose even though Whitman's plans for biology—for all of biology divided up into specialties and then reunited through cooperation—provided a clearly articulated and solid base for both institutions.

By 1894 Whitman clearly had ambitions as high for the MBL as he had for Chicago. He no longer feared competition or objections from the United States Fish Commission in Woods Hole, which had decided not to develop its own research center.[56] The Board of Trustees of the MBL had begun to expand so that some of Whitman's trusted friends joined the primarily Boston-based original group; Henry Fairfield Osborn and Wilson particularly supported Whitman.[57] By 1894 Whitman wanted to expand physiology at Woods Hole as well as at Chicago, and he worked to attract people who would want to join Loeb. Loeb, with his German training, international reputation, and experience at the Naples Zoological Station, clearly appealed to Whitman, despite Loeb's difficult personality, which was to cause problems later.[58] Whitman wanted more people with Loeb's particular approach to biology.

Whether Whitman saw Loeb as extending what he already regarded as the important physiological side of biology or whether Whitman had first articulated a newly acquired sense of the value of physiology only after learning of Loeb's availability remains something of an open question. Whitman's interest in both Loeb and physiology does seem to have developed at the same time. He certainly insisted upon the importance of both morphology and physiology as the two major standpoints of biology at the same time that he realized the value of adding Loeb to his groups. For whatever reasons, Whitman became an advocate of "biological" physiology as a central, and not just a distant, part of biology. He saw Loeb's type of physiology as a particularly desirable model and tried to make both the MBL and Chicago places where physiologists and morphologists could feel comfortable.

PHYSIOLOGICAL MORPHOLOGY

What exactly was that particular form of physiological work that Whitman found attractive? In a set of papers presented as part of the series of evening

lectures at the MBL. Loeb outlined the ideas he had begun to publish in 1891, under the title *Untersuchungen zur physiologischen Morphologie der Thiere.*[59] There he explained what the term "physiological morphology" meant and outlined the basis of his research program: "I have chosen the name Physiological Morphology for these investigations, inasmuch as their object has been to derive the laws of organization from the common source of all life phenomena, i.e., the chemical activity of the cell." Thus such work sought causal accounts of life phenomena in physical and chemical terms. Yet "the aim of Physiological Morphology is not alone an analytical one. It has another and higher aim, which is synthetical or constructive, that is, to form new combinations from the elements of nature, just as the physicist and chemist form new combinations from the elements of non-living nature."[60]

Pauly has focused on this second aspect of Loeb's program. Yet I suspect that only the first part of Loeb's program had any major appeal for the MBL researchers and for Whitman.[61] That MBL audience, especially Morgan, did find this part of the program intriguing. Through his various studies of regeneration and transplantation, Loeb was attacking the fundamental questions about the "physical forces that determine the formation of a new organ," and "How can these chemical forces be brought into relation with the visible changes which take place in the formation of a new organ?" The mechanics of growth would provide the answer to these basic questions of physiological morphology.[62]

Such work fit nicely into the context of emerging German studies in the physiology of development, studies that combined traditional physiological and embryological methods with basic morphological questions. In the process each specialty was changed into something new. These physiological studies had especially attracted the attention of those American biologists who spent their summers at the MBL. In particular, the work on frogs at Jena carried out by Pflüger, Gustav Born, and Roux excited interest. These researchers had picked up on questions raised by Wilhelm His—especially questions about what mechanisms direct organisms and how individual organisms develop. In addition, the suggestions by August Weismann—about the existence of a separate, inherited germ plasm that directed subsequent development of each organism—while convincing virtually none of the Americans, pointed to explanations of how development might be accomplished. Weismann asked not merely what sequence of forms the individual passes through, but how that sequence takes place and through what processes. Such questions concerned function and were thus traditionally physiological, but they also focused on embryos and were thus traditionally morphological as well.[63]

To Whitman, whose Ph.D. dissertation had embraced E. Ray Lankester's suggestion that some sort of "precocious segregation" might occur in the egg cell, such concentration on development and on the causes of differentiation represented an attack on one of the fundamental problems of biology.[64] If Whitman found none of the theories yet put forward completely convincing, he nonetheless saw the value of exploring them further. He had also concluded that development was more complex than simple precocious segregation could explain. In his view, physiologists and morphologists must cooperate to answer those fundamental questions. Like the other researchers at the MBL and like

Loeb, Whitman was more sympathetic to Hans Driesch's and Oscar Hertwig's epigenetic views than to Roux's and Weismann's predeterminism.[85]

Now we can see why Whitman found Loeb's work particularly attractive. Not caught up in detailed studies of how one or another isolated part of the body works, Loeb concentrated on the whole organism—and better yet, on the embryonic organism. Whitman consistently urged the importance of the "organismic standpoint," and it cannot be coincidental that such men as Charles Manning Child, William Ritter, William Locy, Frank Lillie, and Loeb, each of whom worried about how the whole organism works in some way, were all at Chicago while Whitman was in charge. Indeed, I would argue that all were participants in a Chicago school of biology. Whitman's vision, like the Hopkins program earlier, had an important impact on physiology and biology in the United States.

THE NEXT CENTURY

As the Hopkins program faded after Martin's fall, with the rise of the medical school, and as Whitman failed to achieve full support for his programs and turned to his pigeons, the study of biological physiology became increasingly marginal throughout the country. Those physiological morphologists who had found comfortable niches during the 1890s at the MBL and Chicago did not always fit happily elsewhere. Other historical studies, notably the valuable contributions by Robert Kohler and Kenneth Manning, have illustrated what happened to some of the "general" physiologists. Kohler and Manning have also described some of the battles for resources and position that occurred as the biological physiologists struggled to retain their places in biology. In this book, Pauly has further detailed those problems for general physiologists such as Loeb. Specialization on the whole brought divergence, with a loss of the unified perspective that the Hopkins program had preached and the coordination that Whitman had valued so highly. On balance, general and biological physiology lost out as relatively few researchers continued to pursue physiological morphological work. Only Chicago provides a possible exception, with its continuing strong tradition in physiology into this century. Despite promising beginnings, the physiological variants were largely kept out of biology in the twentieth century by scarce resources, increased population density, and the impact of such overzealous individuals as Loeb.

NOTES

1. Allen Kerr Bond, *When the Hopkins Came to Baltimore* (Baltimore, MD: Pegasus, 1927); John C. French, *A History of the University Founded by Johns Hopkins* (Baltimore, MD: Johns Hopkins Press, 1946), esp. pp. 1–26; Hugh Hawkins, *Pioneer: A History of the Johns Hopkins University* (Ithaca, NY: Cornell Univ. Press, 1960), pp. 3–20.
2. Philip Pauly, "The Appearance of Academic Biology in Late Nineteenth-Century America," *J. Hist. Biol.* 17 (1984): 369–397.
3. Daniel Coit Gilman, "The Original Faculty," in *The Launching of a University and Other Papers* (New York: Dodd, Mead, and Co., 1906), pp. 47–56, 51; *Inaugural Addresses* (Baltimore, MD: John Murray, 1876), pp. 15–64, esp. 43; Thomas Henry Huxley, "On the Study of Biology," in *Science and Education* (London: Macmillan, 1893), pp. 262–293, esp. 263.

4. Gilman, "Original Faculty," p. 52; Gilman to Henry Newell Martin, 14 March 1876, Gilman Papers, Special Collections, Milton S. Eisenhower Library, Johns Hopkins University, Baltimore, MD (hereafter, Gilman Papers).
5. Huxley, "Address on University Education," in *Science and Education*, pp. 235–261, esp. 254.
6. Huxley to Gilman, 20 February 1876, Gilman Papers, to recommend Martin; Martin to Gilman, 5 April 1876, Gilman Papers; he declined at first but by 29 May 1876 he had accepted and had outlined a program for Johns Hopkins University; French, *History*, pp. 34–40; Charles E. Rosenberg, "Henry Newell Martin," *Dictionary of Scientific Biography* vol. 9 (New York: Scribner): pp. 142–143; Russell Chittenden, "Henry Newell Martin," *Dictionary of American Biography*, pp. 337–338.
7. Martin to Gilman, n.d., Gilman Papers; Brooks to Gilman, 18 June 1876, Gilman Papers. Brooks explains that he has an offer at the University of Cincinnati but wants to be Martin's assistant; French, *History*, pp. 40–42.
8. Martin to Gilman, n.d., but responds to 29 April 1881, Gilman Papers. For more on Brooks's role see Keith Rodney Benson, "William Keith Brooks (1848–1908): A Case Study in Morphology and the Development of American Biology" (Ph.D. diss., Oregon State Univ., 1979).
9. Rosenberg, "Towards an Ecology of Knowledge: On Discipline, Context, and History," in *The Organization of Knowledge in Modern America, 1860–1920*, ed. Alexandra Oleson and John Voss (Baltimore, MD: Johns Hopkins Univ. Press, 1979), pp. 440–455.
10. Actually, salamanders are particularly appropriate here because one of the principals of this story, Charles Otis Whitman, spent many hours trying to locate the salamander *Necturus* near the Allis Lake Laboratory in Milwaukee. He wanted to study the embryological development of an interesting local species and knew that *Necturus* was alleged to exist in the lake waters of northern Wisconsin. Unfortunately the species proved elusive and, after several futile attempts to locate specimens, Whitman and his student/associate Edward Phelps Allis had just about given up. The local fisherman they had hired insisted that he knew just where to find some of these salamanders: "under almost any stone or stump in the water along the edge of the lake." However, Whitman and Allis had already spent a day overturning every rock in sight and found nothing. They concluded that they had been victims of another "fisherman's story" and that no *Necturus*, or mudpuppies, were to be found there at all. When their hired fisherman, Meyers, insisted that they meet him at 5:00 A.M. the next morning for one last try, they reluctantly agreed, even though they planned to catch a six o'clock train. As Allis later recalled, Meyers had told them: "'You'll find one under that big stone out there in the middle of the race. I see his hole.' Whitman laughed at him and told him he had better go out and find it himself. But Meyers, somewhat nettled, said he wasn't going to get wet to the middle for one of those d—ed things. So I [Allis] told Whitman it wouldn't do any harm to try it; and out he went, trying not to look foolish at allowing himself to be sent on such an errand. He waded out with great deliberation, turning over a few other stones as he went, like a child who wants to make believe that he isn't doing what he has been told to do. Meyers in the meantime had left, saying that he had something to do and couldn't hang around any longer and that if we didn't find a puppy under that stone we would under another a little further out.

"Whitman had now, in his leisurely course, reached the stone he was after and with a smile at me bent down to turn it over. He turned it, then dropped it, and standing up looked at me for a moment. 'There was one,' he said, in an awe-stricken voice. Then he picked up the stone, and without a word brought it ashore and showed me, attached to its under surface, a few large eggs.

'I can't believe it,' he said. 'Why, Mr. Allis, I would give my year's salary for those eggs.'"[10] From Dornfeld, "The Allis Lake Laboratory, 1886–1893," *Marquette Med. Rev.* 21 (1956): 115–144, esp. 126–128.
11. Martin, "Physiological Papers," in *Memoirs from the Biological Laboratory*, vol. 3 (Baltimore, MD: Johns Hopkins Press, 1895); Larry Owens, "Pure and Sound Government. Laboratories, Playing Fields, and Gymnasia in the Nineteenth-Century Search for Order," *Isis* 76 (1985): 182–194, points out the unusual nature of the Hopkins Laboratory. Students and assistants worked together with Martin so that even the major contributions came from the group together rather than from Martin alone.
12. "Class of '90," *Hopkins Medley* (Baltimore, MD: Guggenheim, Weil, 1890), pp. 56–58; these are the students listed in the files of correspondence, Gilman Papers.

13. William Keith Brooks, response in *Science* 3 (1896): 708, to Conway MacMillan, "On the Emergence of a Sham Biology in America," *Science* o.s. 21 (1893): 184.
14. Howell did, for example, as well as others not named. Brooks to Gilman, Gilman Papers.
15. Frederic Schiller Lee, "The Scope of Modern Physiology," *Am. Nat.* 28 (1894): 380–388, esp. 380, 388, and 473–482.
16. After his Ph.D., Lee went to Leipzig for a year, then taught biology at Sarah Lawrence for a year, physiology at Bryn Mawr, and physiology at Columbia from 1891; For more on Lee, see chapter III by Alejandra Laszlo and chapter X by Richard Gillespie, in this book.
17. In addition to Lee's one year at Sarah Lawrence, Henry Herbert Donaldson began in physiology, then received an M.D. degree and eventually moved into a research position at the Wistar Institute.
18. W. Bruce Fye, "H. Newell Martin—A Remarkable Career Destroyed by Neurasthenia and Alcoholism," *J. Hist. Med. Allied Sci.* 40 (1985): 133–166.
19. Allan Chesney, *The Johns Hopkins Hospital and the Johns Hopkins University School of Medicine*, vol. 1 (Baltimore, MD: Johns Hopkins Press, 1943), pp. 230–233.
20. Fye, "H. Newell Martin," p. 161; Gilman Papers reinforce the validity of Howell's convictions.
21. Robert Kohler, *From Medical Chemistry to Biochemistry* (Cambridge, UK: Cambridge Univ. Press, 1982); Chapter 11 discusses biological programs. See also chapter III by Laszlo, chapter XIII by Merriley Borell, and chapter VIII by Pauly in this book on particular programs at Harvard and Columbia in general physiology.
22. Dornfeld, "Allis Lake Laboratory," p. 120.
23. Dornfeld, "Allis Lake Laboratory," pp. 121–124, 133.
24. Whitman to Alexander Agassiz and Anton Dohrn to Whitman, Agassiz Collection, Museum of Comparative Zoology, Harvard University.
25. *MBL Minutes*, vol. 1 (Board of Trustees, 1888), MBL Archives.
26. Brooks to Gilman, 21 June 1889, Gilman Papers.
27. Pauly, "Appearance," 383.
28. Whitman, "Biological Instruction in Universities," *Am. Nat.* 21 (1887): 507–579; esp. 517–518.
29. Cornelia Clapp, "Some Recollections of the First Summer at Woods Hole, 1888," *Collecting Net* 2 (4) (1927): 3, 10; Jane Maienschein, "Agassiz, Hyatt, Whitman and the Birth of the Marine Biological Laboratory," *Biol. Bull. Woods Hole* 168 suppl.(1985): 26–34.
30. In particular by Henry Fairfield Osborn, "The Hereditary Mechanism and the Search for the Unknown Factors of Evolution," *Biol. Lect.*, 1894 (1896): 79–100; "Evolution or Heredity," *Biol. Lect.*, 1890 (1891): 130–141; Whitman to Osborn, Osborn Collection, C. O. Whitman folder, Archives, Department of Vertebrate Paleontology, American Museum of Natural History, New York.
31. Whitman, *Report of the Director*, MBL, 1890, p. 21. Elaborated in "Specialization and Organization," *Biol. Lect.* 1890 (1891): 1–26.
32. Whitman, *Report of the Director*, 1891, pp. 14–17, esp. 15.
33. Whitman, "General Physiology in its Relation to Morphology," *Am. Nat.* 27 (1893): 802–807, esp. 804–805.
34. Whitman, *Report of the Director*, 1892, pp. 29–36, esp. 35.
35. Whitman, *Report of the Director*, 1892, p. 35.
36. Pauly, "Jacques Loeb and the Control of Life: An Experimental Biologist in Germany and America, 1859–1924" (Ph.D. diss., Johns Hopkins Univ., 1980), pp. 127–128.
37. Pauly, "Loeb," pp. 128–129.
38. Kenneth R. Manning, *Black Apollo of Science: The Life of Ernest Everett Just* (New York: Oxford Univ. Press, 1983).
39. Lincoln C. Blake, "The Concept and Development of Science at the University of Chicago, 1890–1905" (Ph.D. diss., Univ. of Chicago, 1966), esp. "C. O. Whitman: The Adaptation of Science," chapt. 4, pp. 122–150.
40. Whitman published *Methods of Research in Microscopical Anatomy and Embryology* (Boston, MA: S. A. Cassine, 1885) following an earlier series of articles about method.
41. Franklin Paine Mall to Harper, 8 February, 7 April, and 9 April 1892, Whitman Collection, University of Chicago Archives, Joseph Regenstein Library, Chicago, IL (hereafter, Whitman Collection, Chicago).
42. Whitman to Harper, 19 December 1891, for example, Whitman Collection, Chicago.

43. Whitman to Harper, memo, n.d., Whitman Collection, Chicago.
44. Whitman looked to Germany for models and for ammunition for experiments, but he also called for particularly American work as well.
45. Whitman to Harper, n.d., Whitman Collection, Chicago.
46. Pauly, "Loeb," p. 130; Loeb to Harper, 30 June 1891, Harper Collection, University of Chicago Archives, Joseph Regenstein Library, Chicago (hereafter, Harper Collection, Chicago).
47. Whitman Collection, Chicago; Whitman Collection, MBL Archives. Whitman had hoped that the endowment would be used for the MBL and an inland research station as well as the University of Chicago. He was bitterly disappointed that his inland station was postponed yet again.
48. Whitman to Harper, letters in Chicago and MBL Archives, throughout the 1890s document his frustration. He got Watase, Wheeler, Loeb, and others in succession.
49. Whitman to Harper, letters in Chicago such as that of 4 September 1899, document this concern. Also, biographical notes about Whitman gathered by Frank Lillie discuss Whitman's growing dismay about the Chicago situation. His letter of 13 March 1896 laments the use of endowment funds to meet basic costs rather than extending resources for biology.
50. Whitman to Harper, 4 September 1899, Whitman Collection, Chicago, in response to a letter from Harper. Quoted with permission from Chicago Archives.
51. Whitman to Harper, 3 May 1899, Whitman Collection, Chicago. Regrets the loss of Wheeler earlier and of impending loss of Watase.
52. Oscar Riddle, ed., *Posthumous Works of Charles Otis Whitman. I. Orthogenetic Evolution in Pigeons; II. Inheritance, Fertility, and the Dominance of Sex and Color in Hybrids of Wild Species of Pigeons*; Harvey S. Carr, ed., *III. The Behavior of Pigeons* (Washington, DC: Carnegie Institution, 1919).
53. Lillie, *The Woods Hole Marine Biological Laboratory* (Chicago, IL: Univ. of Chicago Press, 1944); Maienschein, "Early Struggles at the Marine Biological Laboratory Over Mission and Money," *Biol. Bull. Woods Hole* 168 suppl. (1985): 192–196.
54. Whitman, *Report of the Director*, 1892, pp. 12–13.
55. Whitman to Edwin Grant Conklin, Whitman Collection, MBL. His former Japanese student Chiyomatsu Ishikawa reported, in a biographical sketch translated in the Whitman Papers, Chicago, that Whitman had turned his entire attention to his pigeons, pp. 17–18.
56. Whitman to Conklin, n.d., Whitman Collection, MBL; Brooks to Gilman, Gilman Papers.
57. Whitman to Osborn, Osborn Collection; Whitman to Wilson, Whitman Collection, MBL.
58. At Chicago, Albert Prescott Mathews and Loeb battled over questions of priority, for example, Harper and Whitman Collections, Chicago.
59. Jacques Loeb, *Untersuchungen zur Physiologischen Morphologie der Thiere. I. Heteromorphosis. II. Organbildung und Wachsthum* (Würzburg, Germany: Hertz, 1891, 1892).
60. Loeb, "On Some Facts and Principles of Physiological Morphology," *Biol. Lect.* 1893 (1894): 37–61, esp. 60–61; Pauly, "Loeb," provides a useful summary of those MBL lectures.
61. Pauly, "Loeb," and his book on Loeb with Oxford University Press, in press.
62. Loeb, "On Some Facts," 45.
63. E. S. Russell, *Form and Function* (London: John Murray, 1916), discusses the physiological and morphological traditions.
64. Whitman, "History of the Egg of Clepsine Previous to Cleavage," *Q. J. Microsc. Sci.* 71 (1978): 215–315, esp. 300.
65. Maienschein, "Preformation or New Formation—or Neither or Both?" in *A History of Embryology*, ed. Timothy Horder, et al. (Cambridge, UK: Cambridge Univ. Press, 1985).