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H. N. Martin and W. K. Brooks: Exemplars for American Biology?[1]

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SYNOPSIS. The Johns Hopkins University offered the first modern, American, research-oriented program in biology when it opened in 1876. The program included both physiological and morphological work, so that students could choose either for their advanced degrees. Physiologists studied with Henry Newell Martin, morphologists with William Keith Brooks. Yet students took courses in both areas, and the unique exposure to two lines of research and to two very different sorts of teachers made the Johns Hopkins program exceptional. This paper outlines the dual character of biology at Hopkins, and the particular contributions of both Martin and Brooks. It also argues that the impact of that unique dual offering on four of the more famous students, E. B. Wilson, T. H. Morgan, E. G. Conklin, and R. G. Harrison, strongly influenced the successful and progressive program of research that each chose.

INTRODUCTION

While Keith Benson has concentrated on the creation of an ideal for biology at Johns Hopkins, I want to focus in a different way to emphasize the character of the program and its effect on the product emerging (Benson, 1987). This division of creation and production does not follow strictly chronological lines since it took some time to create and to establish the program fully, and the emerging product evolved through the 1880s and 1890s. Thus, our subject matter overlaps in a few places. Yet while Keith stresses the background and ideals, I concentrate on the relevant features of the program in biology, to illustrate what it was like to have been a student at Hopkins in those prime years in the late nineteenth century. Then I will explore the ways in which a few selected students exhibited their uniquely Hopkins roots.

As Keith has discussed, biology at Hopkins incorporated work in both morphology and physiology. In fact, that bifurcation proved critical in shaping the students' work since the particular blend of influence from physiologist Henry Newell Martin and morphologist William Keith Brooks provided exposure to a then unusual mix of problems and methods for biology. As the yearbook of 1890 recorded, the student who wished to pursue graduate work in biology chose one or the other as a concentration. He

> weighs the respective advantages of physiology and morphology before selecting the field for his life work. He who chooses the first is privileged to ride up and down on the elevator and to breathe the iodoform-laden breezes of the kymograph room, where dwells, attended by his faithful reflex hound, the modest discoverer of the fibres of Sharpey. The morphologist takes his exercise out of doors, and on these balmy spring mornings deems it absolutely necessary to roam over the beautiful hills about Baltimore in search of specimens, which he finally has to dig out of the mud at the brick-yards. A third permissible line of specialization, namely, botany, has always been contemplated since the organization of the biological department, but at present is not available to students. (Class of 1890, 1890)

Indeed, as one critic noted, though there might be plenty of lobster in the Hopkins program, there were scarcely enough vegetables in the Hopkins curriculum to make a decent salad (Swanson, 1951). Zoological physiology and morphology remained the specialties of choice. Graduate students always chose one or the other, or some further sub-specialty as the official field of study for the Ph.D., and never biology gen-

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erally (Brooks, 1896). Nonetheless, the exposure to both and to two quite different research and teaching styles clearly influenced the Hopkins graduates.

HENRY NEWELL MARTIN (1848–1896)

Martin's physiology laboratory concentrated on manipulative experimental work of the sort pursued by his own mentors Michael Foster (1836–1907) and Thomas Henry Huxley (1825–1895). The Irish-born Martin had begun his career as a physician's apprentice, which led him to medical school and then into Michael Foster's physiology laboratory. When Foster moved to Cambridge University, so did Martin. With a scholarship and as Foster's demonstrator, Martin completed the first D.Sci. degree in physiology given at Cambridge in 1875 (Chittenden, 1933). He then moved to the Royal College of Science in South Kensington where he served as Huxley's assistant and compiled *A Course of Practical Instruction in Elementary Biology*. Although only in his twenties, Martin had already become "one of England's most promising young physiologists." Indeed, Huxley urged Gilman that "I do not think that you could possibly have a better man than Dr. Martin" (Rosenberg, 1974). Given the lack of professional opportunities in physiology in England at the time, it is not surprising to find him overcoming his concerns about the lack of proper research facilities in the United States and moving to Johns Hopkins as one of the first six members of the faculty. President Gilman charged Martin with establishing a biology department, a significant choice since American universities did not normally include physiology as a core part of their zoology programs (Pauly, 1984). In particular, Gilman invited Martin "to organize a laboratory & a school of biology, on a plan similar to that of Prof. Huxley at So[uth] Kensington . . ." (J.H.U., Gilman to Martin, 1876; Hawkins, 1960, p. 48).

At Hopkins, Martin quickly set up a successful and productive, even if not prolific, laboratory. There he pursued experiments into the action of the mammalian heart, following along the lines of Foster's work. For example, in one series of experiments he isolated the heart and sustained its beating while testing the effects of artificially manipulated conditions such as temperature, arterial pressure, or ethyl alcohol on the heart beat. Another series of experiments examined the nature of respiration. Antivivisectionists launched the usual attacks, but evidently these remained only verbal since Martin invited any interested parties to visit the laboratory, and there is no record that any critics ever did after the initial housewarming event (Martin, 1876, p. 201; Fye, 1985, p. 147). In thus establishing a research laboratory separate from any immediate medical concerns, Martin was "in a sense a pioneer in the United States, helping to put physiology in its proper relation to the science and art of medicine" (Chittenden, 1933).

Yet perhaps, as one biographer has suggested, Martin really played a more important role institutionally than through the impact of his own research work (Rosenberg, 1974). In teaching, Martin maintained that biology should be studied by way of practical experience and not primarily through lectures. That meant that elementary students should first acquire a solid general background in basic techniques of dissection and microscopy. Then they would move to some lectures on more advanced subjects and would learn to carry out experimental work. At first, this would involve repeating recent experimental work by others, with an eye to understanding the consequences and interpretations. This stage would eliminate what he called the "triflers," who exhibted

> a burning desire to undertake forthwith a complicated research, though they hardly know an ordinary physiological instrument when they see it; much less how to handle it. But they cannot wait; they must begin the next morning, believing, I presume, that laboratories are stocked with automatic apparatus,—some sort of physiological sausage machines, in which you put an animal at one end, turn the handle, and get out a valuable discovery at the other. (Martin, 1884, p. 230)

Only then, after acquiring the basic techniques, should the student move on to do original experimental work of his own.

Martin's program emphasized the acquisition of techniques and the focus on using methods to achieve some sort of discovery. Indeed, advanced students should select "rather specific problems which might be solved conclusively by some new and original method" (Howell, 1908). Rather than exploring alternative ideas or interpretations and rather than developing systems to explain a variety of phenomena, Martin stressed using methods to achieve conclusive results. Most zoologists in the United States at the time did not similarly stress results and methods. Instead they emphasized the importance of familiarity with organisms, as Louis Agassiz did, or the value of exploring theories explaining relationships in organic nature, as morphologist Brooks did.

Martin's emphasis on methods and on results echoes convictions expressed by Hopkins philosopher Charles Saunders Peirce (1838–1914) as well. Peirce stressed that "This is the age of methods; and the university which is to be the exponent of the living condition of the human mind, must be the university of methods" (Hawkins, 1960, p. 223). Science and philosophy should work closely together, Peirce declared, and he set about facilitating that communication. He invited students and faculty to gather around his open fire for discussions in those early years when the Hopkins environment represented, as philosopher Josiah Royce put it, a "dawn wherein 'twas bliss to be alive" (French, 1946, p. 45). The community was small and perhaps Martin and his students actually joined Peirce for those discussions. Martin and Peirce were reportedly good friends (Feibleman, 1946, p. 21). Whether Martin was directly influenced by Peirce, or whether they both responded to similar influences in the Hopkins setting generally, their ideas about what science should do reflect closely parallel commitments. Unfortunately, Peirce suffered some emotional instability, according to his critics, and for a variety of reasons was not reappointed at Hopkins after 1883–1884. This despite reassurances from Gilman and Peirce's expectation that he would be kept on (Hawkins, 1960, p. 195). There is no hint that any other philosophers achieved such sympathy with the biologists as Peirce had, with his pragmatic emphasis on methods and results.

Martin's reputation as a teacher is very mixed. Some praised his teaching qualities. Russell Chittenden, for example, wrote that Martin was a good teacher, "endowed with a pleasing personality, always interested in the welfare of his pupils, sympathetic and with a joyous outlook on life that made him an interesting as well as a helpful companion" (Chittenden, 1933). Walter Meek recalled that "He had an engaging manner, a simplicity and frankness which attracted his elementary students at once," though he retained a greater reserve with advanced students until they showed sufficient interest or ability (Meek, 1928). Charles Rosenberg reported that Martin was a "warm and successful graduate teacher and colleague" (Rosenberg, 1974). And his associate in physiology at Hopkins, William Henry Howell (1860–1945), explained that although Martin "thoroughly enjoyed introducing young students to the beauties and marvels of living structures and their adaptations," for advanced students he adopted a sink or swim approach. "Certainly he could show an extraordinary amount of apparent indifference toward some poor fellow floundering in the difficulties of his first research." Indeed, "Martin was capable of letting them drift in an altogether heartless manner" as he tried to discourage those he regarded as the unfit (Howell, 1908).

As a lecturer, Martin also achieved a less than perfect record. Indeed, he very nearly lost his job or had his salary reduced in 1878, quite possibly because of his poor lecturing (Hawkins, 1960, p. 142). Even students who found him irresistible overall acknowledged that he had a poor delivery, that he was too quiet. But he "had a fascination for his students," particularly those elementary students. And one of those students recalled that he possessed "the most intelligent blue eyes that I have ever seen, and when he was stirred up over some scientific recital they fairly danced with excitement" (Bond, 1927, p. 34).

Martin may have fascinated the students also outside the classroom, as he pursued the informal tradition in those early years

of inviting students to socialize with him. Both he and Brooks "had regular appointments that combined entertainment with a scientific discussion" (French, 1946, p. 79). The student yearbook extolled the advantages of the "scientific-social pipe at the hospitable homes of the professors" (Class of 1890, 1890). In addition, Martin led the Naturalists Field Club, which met on Saturdays at two o'clock to wander about the countryside in order "to study the fauna, flora, and geology of the neighborhood of Baltimore" (French, 1946, p. 47). In the early years, the biology students at Hopkins studied with and got to know Martin, no matter what their particular chosen specialties. By the early 1890s, however, Martin was suffering sufficiently serious alcohol problems that he had effectively withdrawn; he finally resigned in 1893 and died in 1896 (Fye, 1985). Significantly, even at the height of his influence, very few graduate students chose to work with Martin; in the first decades the majority selected instead to concentrate on morphological problems with Brooks (Johns Hopkins University, 1926).

WILLIAM KEITH BROOKS (1848–1908)

The same age as Martin, Brooks had a very different view of biology than Martin did. While Martin stressed experimentation and methods and downplayed the value of theories, Brooks emphasized ideas over methods. In contrast to Martin, Brooks was "an observer and philosopher rather than an experimenter," though as Keith Benson has shown Brooks had no objections to experimentation in principle (Hawkins, 1960, p. 144; Benson, 1979, 1981, 1985). His brother reported that young Will had long loved tramping about the countryside, collecting things, and then organizing them into a museum at home (Conklin, 1910). As physiologist Howell reported, Brooks "was interested in the large problems of biology . . . . Matters of laboratory technique they [his students] might have to acquire from other sources, but from him they obtained the stimulus to real thinking" (Howell, 1909, p. 13). Or as his student and assistant Ethan Allen Andrews put it, "Brooks was not an experimenter but an observer of natural processes, from which he endeavored to interpret logically. He saw too many facts to be long satisfied with the sharp cut result that seemed to follow from experimentally severing some portion of the phenomenon from the rest. He was a recorder of nature and a philosophical reasoner about the outside universe as it appeared to his consciousness." As a result, "from him they [his students] attained the stimulus to real thinking." Further, "His philosophical mind left its impress upon their ways of thought in whatever part of zoology they labored. The old problems of heredity are now attacked by new methods, but some of the foremost investigators are bound to Professor Brooks, more or less intimately, by nurture got when he was a stimulating if not also a formative part of their environment" (Andrews, 1909).

Clearly, then, Brooks exerted a different sort of influence than Martin. Where Martin lectured poorly, Brooks attracted attention with his clear and logical, even vivid and picturesque, lectures. He entranced his students in lectures, but often appeared unsympathetic to the research of his advanced students, claiming absolutely no interest in their daily work. In an approach that actually seems to have worked well, he neglected them and left even the most advanced students to flail about on their own, trying to define their own problems and to discover for themselves what methods might work to help them pursue those problems (Howell, 1909; Conklin, 1910). He concerned himself little with details of laboratory techniques or with practical matters generally. Where Martin offered much regarding techniques and day-to-day guidance, Brooks offered little.

Yet as a teacher and guide to thinking generally, Brooks was clear, logical, and helpful, his students recorded, and though not always socially inclined, he was a wise friend. Those students felt tremendous loyalty to their mentor. Thomas Hunt Morgan wrote to President Gilman in 1891 that he had received an offer to teach at Bryn Mawr and must turn down his Bruce Fellowship. "It is with great regret," he

recorded, "that I find myself adrift from the University and will always look back with pleasure to the four years spent with Dr. Brooks in his laboratory" (J.H.U., Morgan to Gilman, 1891). Another student, Edmund Beecher Wilson, had studied with Martin as well, but found himself more in sympathy with Brooks's approach. As he recalled later,

> "It was through informal talks and discussions in the laboratory, at his house, and later at the summer laboratories by the sea that I absorbed new ideas, new problems, points of view, etc." "Through him I first discovered what I really wanted to do." "From him I learned how closely biological problems are bound up with philosophical considerations. He taught me to read Aristotle, Bacon, Hume, Berkeley, Huxley; to think about the phenomena of life instead of merely trying to record and classify them." (Morgan, 1942)

Those students especially enjoyed the summers at the Chesapeake Zoological Laboratory, which Keith Benson has described (Benson, 1987). Brooks produced an atmosphere which stimulated thinking, even as it forced the students to work out their daily research routines and to discover useful methods on their own (McCullough, 1969).

Martin and Gilman had hired William Keith Brooks after they had decided to hire a second biologist with a concentration in Comparative Embryology. Alexander Agassiz had recommended Brooks for his comparative and marine studies, both of which Agassiz regarded as central to good embryological work (J.H.U., Gilman file on Brooks, May 1876; Swanson, 1951). Brooks had completed his B.A. at Williams College, with a hefty dose of reading in philosophy, then his Ph.D. at Harvard, where he had attended a session of the Anderson School of Natural History on Penikese Island. Brooks had all the elements of a solid traditional background in morphology. Since the six original professorships had been filled, Martin and Gilman appointed him as a Fellow in Johns Hopkins' unique fellowship program designed to attract the best young men to postgraduate work at Hopkins. According to one opinion, "Probably no expenditure of ten thousand dollars in American education has ever had so large and so enduring a return from the investment" as that fellowship program (French, 1946, p. 41). Brooks certainly was one of the successes—but not exactly as a Fellow. In fact, he received an immediate promotion to the position of Associate in biology, with the mandate of teaching the morphological side of biology while Martin continued with the physiological.

The Relations of Physiology and Morphology

Martin and Brooks worked together, but they recognized the differences in their subject areas and sometimes their differences produced disagreements about relative allocations of resources. Philip Pauly has suggested, in his excellent survey of biology programs in late nineteenth century America, that morphology was really intended to play a secondary role to physiology because the latter served Hopkins' ultimate cause of promoting medicine (Pauly, 1984). I find the evidence inconclusive that Gilman intended morphology to play a secondary role; nor is it clear whether Martin did. He emphasized the autonomy of the various biological specialty areas, for he "thought consistently in disciplinary terms; he never lost sight of his identity as a physiologist . . ." (Rosenberg, 1974). In particular, he wanted to ensure physiology's separation from clinical medicine, but he also saw its independence from morphology. As Martin wrote to Gilman, Brooks should not be considered his assistant in biology. Rather, "Morphology and Physiology are as distinct subjects as Chemistry and Mineralogy—they are allied, but different" (J.H.U., Martin to Gilman, n.d., probably 1886).

Again in 1881, in a detailed report to Gilman recording the department's needs, Martin reiterated the separation of specialties and suggested a priority for Hopkins's development. In preparation for the opening of the medical school, all aspects of the biological program should be in

place, he urged. Physiology should come first, because of its service to medicine but also because it was least developed elsewhere in the United States, while botany and comparative anatomy could wait. These areas could come with normal increases in the university staff. "Physiology, on the other hand, I believe to have a special claim at present." He acknowledged that the Chesapeake Zoological Laboratory had proven its value but that

> (subject as the opinion will be to the deduction that I am prejudiced in favor of the branch of biological study for which I have the strongest personal preference) I think it would be a pity to devote funds which may be appropriated for the biological department of the University to the further development of the Marine Laboratory until the physiological work in Baltimore has been placed on the best possible footing: it is best to first do one thing thoroughly well; and then take up the next. (J.H.U., Martin to Gilman, 1881)

I do interpret this as an indication, at least in part, of Martin's prejudices; he clearly did protect the interests of his own specialty area first. But it is not clear that he regarded morphology as of less value for biology in the long run.

Martin's feelings undoubtedly contributed to the way in which physiological and morphological work remained effectively separate at Hopkins. Despite all the rhetoric when the department began about the great new program in *biology* as a whole, graduate students did not receive their degrees in the general field but in some defined subset. Brooks explained that "among all those who have been recommended for this [Ph.D.] degree during the last twenty years not a single one has presented himself for examination in biology, although many have been examinzed in various branches of biological science" (Brooks, 1896).

So what did the students get from their Hopkins experience? Did they really profit from the dual emphasis on the program? Does the particular character of the program explain the fact that such outstanding leaders in biology as Wilson, Morgan, Conklin, and Harrison all emerged as products? One historian claims that "the system was rigorous and the selection intense," but the fact that such men "were among the finished products is proof enough that Gilman and his faculty knew what they were doing" (Swanson, 1951). Others suggest that the success was more accidental, a case of all the necessary ingredients all being in the same place at the same time (McCullough, 1969, pp. 437–438).

The evidence strongly suggests that their dual exposure to physiology and to morphology did directly and crucially influence at least the four individuals mentioned above. Student files in the Hopkins Archives demonstrate that Morgan and Harrison each took healthy doses of course and laboratory work in physiology as well as in morphology. Conklin's and Wilson's own notes about their education suggest similar exposure to physiological work, though they may perhaps have concentrated earlier in morphology. Since physiological study remained very rare in biological programs in the United States as Martin had emphasized to Gilman, this conjunction was unusual (J.H.U., Martin to Gilman).

I believe that the conjunction of two areas of research, exemplified by such different individuals and such different research programs as Martin's and Brooks's, did crucially influence the course of their students' biological work. Though Hopkins did not claim that its students had mastered all of biology, these students really did master biological approaches generally. In effect, they each embraced the sorts of problems and the concern with broader interpretations that Brooks exemplified, while they each eventually, in different ways, incorporated the disciplined, experimental laboratory techniques and methods that Martin and his assistant and eventual successor William Howell exemplified. I will outline briefly the early work of each of these four leaders in zoology, looking specifically at the ways in which either Mar-

tin or Brooks acted as exemplar for each. Others in this symposium will turn to later periods of their work, after each had moved on to his own specialized research program in, respectively, cytology, embryology, or genetics.

THE STUDENTS

Born in 1856 in Illinois, Edmund Beecher Wilson (1856–1939) loved animals and music. At sixteen, he had a "great experience" teaching in a one-room, wood-stove-heated stereotypical rural American schoolhouse, but he determined to enter college after that year. A Ph.B. from Yale's Sheffield Scientific School and a summer with Spencer Fullerton Baird (1823–1887) dredging for marine life with the U.S. Fish Commission provided Wilson's preparation for Johns Hopkins graduate school work in biology (Morgan 1941, 1942; Muller, 1943).

Entering Hopkins in 1877, Wilson settled quickly onto the driving problem for his research: how does the individual exist in the germ? This concentration took him to Brooks, who particularly emphasized the value of marine study. Thus, Wilson joined the Chesapeake Zoological Laboratory group in 1879 and 1880, then served as Brooks's assistant for the next two years. Brooks recorded in a progress report to Gilman that Wilson amused the natives tremendously by wearing a progressive short bathing suit, so that "The colonial people have a profound admiration for Wilson's legs, and speak of them in the warmest terms" (J.H.U., Brooks to Gilman, 1880). Wilson completed his Ph.D. in 1881 with his study of metamorphosis from the larval stage of a marine worm, the *Actinotrocha*, work which followed closely the model of Brooks's own morphological study of the same time (Wilson, 1881). The dissertation examined the later stages of metamorphosis, demonstrating that the apparently radical changes result from relatively simple and minor adaptive alterations. Wilson was concerned both with the mechanism by which metamorphosis occurs and with the evolutionary explanation of why that mechanism might have come into play historically. The latter question came clearly from the morphological tradition and would have seemed quite foreign, or even irrelevant, to Martin.

Yet Martin's influence also exhibited itself. When Wilson made the then-traditional pilgrimage to Europe after graduating from Hopkins, he took with him a letter of introduction from Martin and visited the great physiological as well as embryological laboratories of the day (J.H.U. Archives, Student File, 1883).

Wilson did not simply follow Brooks in his research. Since his undergraduate days at Yale, Wilson had also been strongly interested in the work of Harvard professor Edward Laurens Mark (1847–1946) who, Wilson recorded with some astonishment, "has written two hundred pages about the development of the snail and has only got so far as the 2-cell stage" (Morgan, 1941, p. 318). That work attracted him to early developmental stages, before formation of the germ layers which most morphologists regarded as the really significant starting point for embryonic development (Baxter, 1974, 1976, 1977).

That interest in early stages Wilson pursued at the Marine Biological Laboratory in Woods Hole, Massachusetts, probably the most important formative influence beyond Hopkins. There he pursued his classic studies of cell lineage, of homology, and of cytology, all of which reflected a style of morphological study and of broad philosophical concerns strongly reminiscent of Brooks (Maienschein, 1978). Like Brooks, Wilson asked questions, then detailed his observations and drew comparisons that underscored common phenomena to answer the questions at hand. Like Brooks, he recognized the value of pursuing an hypothesis as a useful explanation of the phenomena. Yet unlike Brooks, Wilson was not willing to venture onto quite such speculative ground in order to have an hypothesis, nor was he as centrally concerned with constructing phylogenies. As biology generally moved toward more experimental work and away from the speculative excesses of phylogenizing, so did Wilson, who began to exhibit more

directly some of the laboratory techniques that he may have absorbed from his physiological study.

Ten years after Wilson's birth, Thomas Hunt Morgan (1866–1945) was born in Kentucky. He also exhibited an early interest in natural history, taking fossil collecting trips through the surrounding areas and joining mountain field trips in the summers. After receiving his B.A. from the State College of Kentucky (now the University of Kentucky) in 1886, Morgan attended a summer session of Alpheus Hyatt's (1838–1902) school at Annisquam, Massachusetts. There he encountered traditional natural history study, methods of collecting and dissecting, and marine study. Intrigued, he went on to Johns Hopkins for graduate work (Sturtevant, 1959; Allen, 1978).

There he began to work with Brooks, but also felt a strong attraction to physiological laboratory experiments. His early concern was essentially the same as Wilson's, namely how does the individual exist in the egg, or how does it emerge from the egg? He also recognized the value of concentrating on marine organisms. Yet he saw those problems less in evolutionary terms, as Wilson did, than as problems of heredity and development.

Morgan's biographer Garland Allen has emphasized the importance of Morgan's rejection of Brooks's tendency to speculation and thus of morphology more generally (Allen, 1978). Yet I do not see any such rejection through Morgan's early years of research. While Morgan at times certainly lost patience with Brooks's emphases or with his style, he stuck with him and continued to work on problems closely allied to Brooks's. He did not turn to work with Martin, nor did he reject the sorts of morphological questions Brooks had influenced his students to ask. Morgan worked at the Hopkins table at the U.S. Fish Commission in Woods Hole in 1890, then completed his Ph.D. in that year. The next year he spent as a Bruce Fellow and spent two summers helping to organize the Chesapeake Zoological Laboratory sessions. Surely Morgan had not rejected the value of the sort of morphological or marine work that Brooks did.

After Hopkins, he also spent his summers at the Marine Biological Laboratory in Woods Hole, exchanging ideas with the best of American biologists, physiologists and morphologists alike (M.B.L. Annual Reports, 1890s). Morgan's research of the early 1890s very strongly reflects the influence of his Hopkins upbringing and does not show any rejection of Brooks's problems or approach. Indeed, Morgan's early papers sound even more like Brooks's than Wilsons's, with Wilson's early emphasis on earlier development stages. Morgan considered the fate of the blastopore in amphibians, for example, organisms which he could acquire more easily during the year than marine species. He concluded that "these propositions give good evidence to support the view that in Amblystoma [now *Ambystoma*] we have found a form which retains during its larval development for a short period the ancestral conditions of the blastopore." And "It seems to me that the following hypotheses or suggestions may at least tentatively be proposed . . . , that in Amblystoma we have in the behavior of the blastopore the changes which have in general taken place in the phylogeny of that organ" (Morgan, 1889). Heredity and evolutionary phylogenies, development and adaptation: these provided Morgan's focus as they did Brooks's well into the 1890s. Yet by the late 1890s, Morgan had turned to more manipulative and more closely analytical research reminiscent of Martin's as he became intrigued by his colleague Jacques Loeb (1859–1924), by Hans Driesch (1867–1941) at Naples, and eventually by problems of sex determination (Allen, 1978; Maienschein, 1984). Indeed, Morgan had first learned from Martin "to appreciate physiological approaches to biology" and "was even inclined to turn to them rather than to Brooks at times" (Sturtevant, 1959). It was then, in retrospect, that Morgan acknowledged Martin's influence as well as Brooks's.

Born in Ohio and brought up in a religious family, Edwin Grant Conklin (1863–

1952) felt a lifelong concern to show the compatibility of biology, especially evolutionary biology, and religion. His life on the farm had given him an interest in natural history and the outdoors that was reinforced by undergraduate collecting trips at Ohio Wesleyan University, from which he received his B.S. in 1885 and a B.A. in 1886. Then, like Wilson, Conklin taught school in a one-room school district, an experience which he also regarded as one of the most valuable of his life. After teaching for three additional years at Rust University, a black college in Mississippi run by the Freedman's Aid Institution of the Methodist Church, Conklin entered Johns Hopkins to study biology. He, too, took courses from both Martin and Brooks, quickly aligning himself with the morphological side under Brooks (Butler, 1952; Harvey, 1958).

Conklin found Brooks's evolutionary emphasis and philosophical bent appealing, perhaps more than any of Brooks's other students. Conklin's substantial biography of his advisor demonstrates his feelings (Conklin, 1910). As he also noted elsewhere, "I cannot begin to describe adequately the stimulus for scholarly work and research which I received at Johns Hopkins. It was as if I had entered a new world with new outlooks on nature, new respect for exact science, new determination to contribute to the best of my ability to 'the increase and diffusion of knowledge among men'" (Harvey, 1958).

Though Conklin thus considered himself indebted to Brooks and the atmosphere at Hopkins, he also acknowledged that he had often been left on his own in his research. Indeed, Brooks had sent him off to the U.S. Fish Commission table in 1899 to work on the oyster, suggesting that Conklin trace its embryological development and behavior, a traditional sort of morphological work. Unfortunately, the species that Brooks suggested did not exist in the colder waters of Woods Hole. Conklin therefore turned to gastropods, focusing on the slipper snail *Crepidula* (Conklin, 1968).

In Woods Hole he became interested in the earliest developmental stages as Wilson had. Conklin even began following development cell by cell, then soon discovered that Wilson across the street at the Marine Biological Laboratory was pursuing a similar study. Termed cell lineage work, or cell counting, by critics, this study of early stages did not seem important to Brooks, who held that "There is no morphological significance in the mere duplication of parts. The cleavage of the egg is a mere duplication of cells and I do not think it has any morphological significance in it." Of Conklin's thesis, Brooks said skeptically, "This university has accepted theses on counting words. I suppose it might accept one on counting cells" (Harvey, 1958). Yet that study of *Crepidula* and later similar work on ascidians became classics (Conklin, 1897, 1905). The way in which Brooks left his advanced students on their own in their day-to-day work may very well, as McCullough suggests, have actually been a strength of his teaching style (McCullough, 1969). They did somehow learn to do progressive morphological studies and did also learn laboratory techniques from their Hopkins education.

The youngest of our four, Ross Granville Harrison (1870–1959) illustrates a different sort of product from Hopkins. He had lived in Baltimore most of his life, enjoying walks in the countryside and gaining an early curiosity about living beings. Unlike the others, he entered the local John Hopkins for undergraduate study, intending to follow a premedical program. Thus, he studied physiology with Martin as an undergraduate and even credited Martin with having attracted him to biology (Nicholas, 1961, p. 135). After graduating, however, he decided to continue with graduate work in zoology rather than turning to medicine or staying with physiology.

Like his colleagues, Harrison also found embryology particularly intriguing: how *does* that egg become a complex differentiated individual? Careful observation, thorough knowledge of the recent literature, and familiarity with natural history Harrison learned from Brooks. Marine study he experienced at the U.S. Fish Com-

mission with Conklin in 1890 and at the Chesapeake Laboratory in Jamaica in 1891. Yet, unlike his fellow students, Harrison retained a strong interest in medicine and a strong attraction to the methods and questions of Martin's physiology (Maienschein, 1978, 1983). Harrison traveled to Germany to study and settled in Bonn with Moritz Nussbaum exploring later developmental stages, particularly the development of symmetry in teleosts. After a year in Germany, Harrison returned to Hopkins to complete his degree. But he wanted to go back to Germany. He therefore applied for a Bruce Fellowship from Hopkins, explaining that he wished to study methods in Germany. Brooks reported to Gilman that he did not altogether approve of Harrison's desires, and that he did not believe that Harrison needed to learn new methods:

> I do not thoroughly approve Harrison's plan to study in Germany as Bruce Fellow until Jan. 1st but I have no doubt he will make good use of his time and I do not wish to object although I should prefer to see him use the methods at his command for the production of results, rather than to devote his time as Bruce Fellow to new methods. (J.H.U., Brooks to Gilman, 4 September 1893)

In a letter to Gilman, Harrison reaffirmed that wish to use his Fellowship in order to acquire the latest methods:

> My object in so doing is that I may spend some months in the laboratory of Professor Flemming in Kiel, where I may best become acquainted with the latest methods in cytological research, and where I may follow out to the greatest advantage my present work. . . . and under the conviction that by following it I shall derive the greatest possible benefit for my future morphological studies. (J.H.U., Harrison to Gilman, 6 August 1884)

Harrison clearly did value familiarity with methods in a way that had been reinforced, if not initiated, by Martin and then Howell, more than by Brooks. Though his dissertation and early publications did not show any familiarity with those cytological methods which Harrison had mentioned to Gilman, that study of teleost symmetry and his next series on nerve fiber development represent a fine blend of the two sides of that Hopkins biological program (Harrison, 1893, 1898, 1910).

Each of these four students went on to other work. Indeed, each founded a strong and successful research program of his own by 1910. Given their similar backgrounds at Hopkins and at the Marine Biological Laboratory, the divergence of those programs is intriguing and at first surprising. But recalling the dual nature of that Hopkins experience helps to explain the particular directions chosen and the blends of problems and methods reminiscent of morphology and physiology, exemplified by Brooks and Martin.

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