AN ABSTRACT OF THE THESIS OF

Keith Rodney Benson for the degree of Doctor of Philosophy

in General Science (Biological Science) presented on April 26, 1979

Title: WILLIAM KEITH BROOKS (1848-1908): A CASE STUDY IN MORPHOLOGY AND THE DEVELOPMENT OF AMERICAN BIOLOGY

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Abstract approved: ______________________
Paul Lawrence Farber

The major historical studies that have examined American biology have emphasized the development of experimental biology at the end of the nineteenth century. In this characterization, the descriptive branch of biology has often been treated as less than important and, in several cases, as a hindrance in the application of experimentalism to biology. As a result, one is often left with the impression that morphology and experimental biology represented two conflicting aims in biological investigation.

A more balanced appraisal of the development of American biology can be obtained by examining the biological community in the last half of the nineteenth century. William Keith Brooks (1848-1908) was selected as a case study. Brooks was America's major morphologist. As such, his scientific work mirrored the twin goals of morphology; to describe the form and structure of organisms and to elucidate any possible ancestral relations of the organisms. In the last half of the century, embryological investigations or life

histories were considered to yield the most information on the organism's ancestry. This followed from the widespread acceptance of the biogenetic law (ontogeny recapitulates phylogeny) and the acceptance of evolution theory. Brooks's own work fits into this characterization of morphological investigation. His studies were primarily upon the life histories of molluscs, hydromedusae, tunicates, brachiopods and crustaceans. In addition to carrying out an active research program, Brooks also dealt with several of the major problems facing morphology. The most critical problems were (1) developing an exact criterion for homology, the basic tool for phylogenetic reconstructions and (2) accounting for the facts of heredity and variation, upon which the theory of descent was based. Brooks's treatment of both of these problems provides an indication of his central position in American morphology. Brooks's position in the development of biology in the United States becomes even more central with an examination of his professional position. As a member of the original Biology Department faculty at Johns Hopkins University, the first graduate program in biology in America, Brooks trained a whole generation of American biologists. While several of these scientists remained morphologists, several others were important in the new application of experimental techniques to biology.

The study of Brooks, his scientific work, his role as a morphologist, his position at Johns Hopkins and his response *vis-a-vis* the rise of experimentalism in biology reveals that the standard interpretation of late nineteenth-century biology is largely inaccurate. It is much more instructive to understand the role of descriptive biology and experimental biology in the development of American biology as being complementary.

William Keith Brooks (1848-1908): A Case Study in Morphology and the Development of American Biology

by

Keith Rodney Benson

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Completed 26 April 1979

Commencement June 1979

APPROVED:

Redacted for Privacy

Associate Professor of History of Science in charge of major

Redacted for Privacy

Chairman of Department of General Science

Redacted for Privacy

Dean of Graduate School

Date thesis is presented 26 April 1979

Typed by Leona Nicholson for Keith Rodney Benson

ACKNOWLEDGMENTS

Perhaps because this study was originally started in 1976 there are many people who have become involved with it. To them I would like to express my gratitude in more than a perfunctory manner. Indeed, many of their contributions have been of a most significant nature.

Charlie Miller of the School of Oceanography at Oregon State deserves special mention. It was at his suggestion that I gained my first exposure to W. K. Brooks. Charlie's subsequent interest in the project, his criticisms of the initial stages of the study and continued encouragement through his example of fine scholarship, have all been important to my work.

During a research trip to the East Coast in 1977 I benefited from the kind attention I received at several libraries. I would like to express my thanks to M. C. Beecheno in the Manuscripts Department of the Eisenhower Library at Johns Hopkins University, Ann Farr of the Firestone Library at Princeton University, Murphy Smith of the American Philosophical Society Library and Jane Baldwin of the Museum of Comparative Zoology Archives. Special thanks are due to Julia Morgan in the Ferdinand Hamburger, Jr. Archives of Johns Hopkins University for her interest in this study and her many suggestions concerning the existence of material pertaining to the work. I would also like to express my thanks to Robert Donnell of the Kerr Library at Oregon State for his assistance.

To Jane Maienschein, Ron Rainger and Scott Gilbert, I extend my appreciation for their attention to the work, for the stimulation I have received from their own studies and for the many helpful comments and criticisms we have shared.

I shall always be grateful for the kind support I have received at Oregon State University. Dr. David Willis has been most generous in terms of material support and encouragement. For intellectual stimulation, I have benefited from my association with the members of the "Institute," Brookes Spencer, Jim Morris, Dan Jones and Paul Farber. The Wednesday evening "Dinner-and-Reading Club" consisting of Joel Hagen, Marshall Allen, David Chapin and Paul Farber has been an important center for discussion and criticism, as well as most enjoyable company. To the many graduate students who contributed to a sense of empathetic comaraderie, I extend my special thanks.

My debt to Paul Farber is of a special nature. From a long and satisfying association with him, I realize that my intellectual development has been the result of his efforts. His example of dedication and commitment to scholastic work has been a constant source of emulation. His encouragement always has been a stimulating factor. His suggestions, criticisms and optimism concerning my work have often given me the necessary inspiration to continue the work even when the study appeared most difficult. And, the warm relationship that I have developed with him has been a steady source of comfort and aid. In short, it is with a deep sense of appreciation and gratitude that I recognize Paul's

contributions to this study. Vreneli Farber has also contributed importantly by supplying the most wonderful meals that have often spawned an evening of fruitful discussion.

Finally, I should make mention of some very special people. Several of Brooks's relations, especially Amasa B. Ford, have shown an interest in the study and have contributed to my understanding of Brooks's personality through personal reminiscences and family manuscript materials. Laurie Benson has been a most understanding person throughout this study and has endured my company even during the most difficult of times. Leona Nicholson has generously offered her services as a typist, but has also made valuable contributions as a critic. Her support through our years of association has been of an invaluable nature. Finally, a special thanks to Babs O'Connell for providing me with the necessary sense of confidence to undertake a venture of such a magnitude. I only hope someday to be able to reciprocate.

To all those mentioned above and others who I may have forgotten, my deepest appreciation is extended. My only hope is that the quality of this dissertation will reflect the quality of their contributions.

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INTRODUCTION

Traditionally, the primary focus of historical studies concerning nineteenth-century biology has been directed toward developments in Europe. In the recent past, however, several historians have turned their attention to the United States. The result has been a marked increase of interest in the development of American biology in the nineteenth century and a related increase in the number of historical studies on this topic. In the main, these studies reveal a distinct bias by historians of biology for stressing only a few themes.[1] A dominant area of interest has been studies of the impact of Darwinism on many phases of American culture. This area of investigation has become so popular that the title of "Darwin industry" has been applied to describe the extent of the studies. A second theme that has received much historical attention has been the rise of experimentalism in biology. Of paramount interest in these studies have been developments leading to and coming from the experimental studies at the Marine Biological Laboratory at Woods Hole dating from the late 1880's. The last major historical theme deals with the developments in the late nineteenth century that were to prove to be most influential in the new fields of genetics and heredity in the early twentieth century. The interest exhibited by several historians in this subject has led Donna Jeanne Haraway to characterize many of the studies focusing on this period as "genetic-o-phillic" [sic].[2]

The cumulative result of this overwhelming preoccupation that historical studies of the nineteenth century have demonstrated for Darwin, experimentalism and genetic developments, has been a glaring paucity of careful examinations of the period in American biology between 1860-1890. Consequently, the exact character of biology and the exact nature of the biological practices during this period remains shrouded in obscurity.[3] In particular, the descriptive work in embryology, anatomy and paleontology, the three major areas of interest in biology at this time, have been generally ignored. Such an omission is significantly critical because developments in these fields were to play major roles in the growth of biology at the end of the nineteenth century. In addition, it was under this descriptive program in biology that most of the leading practitioners of late nineteenth- and early twentieth-century American biology were trained. Any comprehensive study of American biology or investigation of the work of American biologists in the late nineteenth century demands careful attention to these descriptive disciplines of biology.[4]

The present study will be restricted in scope to a detailed examination of the descriptive studies in embryology conducted between 1875-1900.[5] It was in this area of morphological investigation that many of the problems and questions of the more experimental studies of the 1880's and 1890's were first raised. Embryology also contributed many of the refined techniques and practices that were to become valuable to more experimental work.

It was also in the field of embryology that the most impressive and influential experimental work was first applied in the 1880's. Subsequent work proved to be so fruitful and exciting that the new field of experimental embryology became a prominent addition to biological study in the 1890's.

Despite the central role that embryology was to play in the experimental programs, its development outside of an experimental context has not been adequately addressed. Specifically, when references are made to the period immediately preceding the 1890's, they usually stress the alleged engrossment that the American biologists had for extravagant speculations concerning the ancestry of organisms. Roberta Beeson eloquently states the prevailing interpretation.

> Modern historians of biology have shown little interest in the problems of evolutionary reconstruction, and their characterizations and evaluations of the phylogenetic period fail to convey the complexity of the issues involved in such problems as the search for Vertebrate origins. Although most scholars acknowledge that phylogenetic research played a major role in the growth of anatomical and embryological knowledge between the 1860's and 1880's, their descriptions of the period leave the impression that extravagant speculation was the major activity of the early evolutionists, and that practitioners of evolutionary reconstruction made no significant contributions to the conceptual developments of biology.[6]

While speculation upon the ancestry of organisms was one of the aims of the morphologist, it in no way represented the totality of morphological studies. Furthermore, by stressing the "extravagant" nature of morphology, a serious inaccuracy concerning the development of the field and its possible importance for later work of a more experimental nature, has resulted. Developments in descriptive embryology were made prior to the 1890's that perfected the descriptive techniques and historical explanations embryology employed. There was a definite refinement illustrated in these studies from 1860-1890. Investigators sought to bring their descriptive work in harmony with the advances in cell theory and evolutionary theory. Work that focused on the organ and tissue level in 1860 was modified to the extent that germ layers and cell fates became the primary areas of interest in the 1890's.

By examining the development of descriptive embryology between 1875-1900, this study will attempt to accomplish two goals. The first will be to provide a detailed appraisal of what it meant to be a morphologist in nineteenth-century America. This approach will begin with the development of morphological studies in America prior to 1875. By presenting the state of morphology at this time, the necessary background will be given against which later developments can be contrasted. This examination will look at the major problems confronting morphology; it will examine the practices and techniques that were used to look at these major problems; and it will evaluate the successes and failures of the morphological approach in dealing with the problems facing it. More importantly, by examining the state of morphological studies from a period prior to 1875 through the 1890's, it will enable one to trace the development of the discipline. Careful attention will be directed toward the role that morphological studies in embryology had in the development of the more experimental studies in the 1890's.

The second goal of this study will be to provide a revision to the standard interpretation of the relationship between morphology and experimental biology. Typically, the speculative phylogenetic aspect of morphological investigation has been stressed in discussions of the history of morphology. Seen in this light, morphology has been depicted as an outmoded and, in many cases, an unproductive field of study. In particular, because of this character, it has traditionally been regarded as having little to offer the later experimental studies. Several of the major historical treatments of this period reflect such a viewpoint. In Biology of the Nineteenth Century, William Coleman states that the morphological approach became inappropriate for providing direction for biological investigation precisely due to the speculative nature of the enterprise.

> The limitations of this approach [ancestral-embryonic parallelism] were increasingly evident by 1875. A decade later this low-voiced criticism was converted into a forceful program for a new approach to problems of individual development. No longer might historical explanation, drawing exclusively on descriptive and comparative embryology, suffice for understanding individual development. That understanding would henceforth come from the analysis of causal factors, meaning essentially the appropriation of physico-chemical techniques and explanatory principles heretofore neglected by morphologists. Grounds were being laid for the transformation of embryology into an experimental science.[7]

Garland Allen echoes a similar position concerning the studies in morphology.

> The considerable speculation and grandiose theories that made up the bulk of evolutionary theory reflected this lack of rigorous proof and confounded in a serious way an easy and thorough understanding of Darwinian theory. . . . By the 1890's biologists working in areas outside of physiology had become

> exasperated with the aims and practises of morphology. They opposed the dominant role that Darwinian theory had come to play, excluding as it did many other areas (such as embryology) that had an inherent interest of their own.[8]

Allen claims that Wilhelm Roux (1850-1924) and the new program of Entwicklungsmechanik or mechanical development,

> . . . swept aside the old preoccupation with evolutionary questions and, as an alternative, raised a problem belonging to embryology alone; the mechanism by which embryos grew and differentiated. . . .[9]

Jane Oppenheimer characterized the development of American biology by claiming that the phylogenetic work of the morphologists was a stumbling block to progress in embryology and the experimental program in biology.

> It [biogenetic law] was considerable, and acted as a delaying rather than an activating force; and it was stifling to immediate progress, since embryologists were for many years after to examine embryos primarily to establish evidence of phylogenetic relationships. . . . progress in terms of new concepts was necessarily impeded.[10]

All of these contemporary historians of biology have accepted a similar position stressing the speculative nature of pre-experimental biology. Such an interpretation can be traced at least as far back as to Erik Nordenskiöld's (1872-1933) classic, History of Biology (1929).[11] He, too, was impressed by the emergence of experimentation from studies of a speculative nature.

> Modern heredity-research has introduced quite a different and essentially experimental treatment of the problems of evolution, and the old morphological speculation upon the origin of species and genera has proportionately lost ground--as it has always happened in the history of the exact sciences that speculation must give way to facts.[12]

> As a result of exact heredity-research the theory of evolution has itself been directed along other lines; phylogenetical

> speculations have for the most part been abandoned--at least for the time being.[13]

The common impression that these scholars have given of the rise of experimental studies in biology is that experimentation implied a revolt from the questions, methods and aims of morphological studies. In particular, by emphasizing the speculative nature of descriptive work, a serious inaccuracy has been created concerning the change in the character of American biology in the late nineteenth century. The American biological community has been depicted as operating under the aegis and constraint of the biogenetic law until the early 1890's. At this time, a new approach utilizing experimental investigations of embryological problems ushered in a new period in biological investigations. This interpretation fails to appreciate the significant influence the morphological program in embryology had on the new studies. It also fails to take note of the fact that descriptive embryology continued as a viable tradition in biology throughout the end of the nineteenth century and into the twentieth century. In fact, such descriptive work provided essential material for the work of the experimental biologists. As E. B. Wilson (1856-1939) stated in 1895,

> I do not belong to those, who, impressed by the rich fruits and still greater promise of the experimental method, regard the past achievements of comparative morphology as labor lost, and look forward with indifference to its future. In its present methods are defective, they must be refined; but the great body of facts it has accumulated, and will accumulate hereafter, will always form the very framework of biological science.[14]

Wilson's views concerning the importance of descriptive approaches in biology represents a much more meaningful interpretation of the late nineteenth century than the view that such studies contributed little to the development of American biology. To provide an accurate picture of the relationship between morphology and experimental biology, one must stress the continuity between the two approaches.

This study will use William Keith Brooks (1848-1908), who was the major American descriptive morphologist between 1875-1900, as a case study to accomplish the dual purpose of characterizing morphological studies in embryology in the latter half of the nineteenth century and providing a more accurate appraisal of the relationship between morphological investigations and experimental studies in biology. Brooks was chosen because of his central position in American biology. He served as a faculty member in the Biology Department of Johns Hopkins University from 1876-1908. His work as a morphologist provides an illustration of what the major problems of morphology were, and of the development of the discipline in the late nineteenth century. His influential role as the instructor of many of America's premier experimental biologists provides added interest to an examination of his crucial role in the development of American biology.

In presenting a detailed account of the work of W. K. Brooks, this study will indicate that speculations upon questions of phylogeny represented only one component of morphological work. In embryology, much of the descriptive work carried out under the guidelines of morphology was continued by the experimental embryologists. At the same time, this thesis does not deny that there were important changes in the character of embryological work that took place between 1875-1900. However, this change cannot be described as a simplistic break from a morphological approach to an experimental approach. Instead, a much more complex situation existed in the 1890's. Questions confronting the embryologists using strictly descriptive methods became irresolvable with these traditional strategies. It was to these problems that the new experimental approach in embryology was to prove so successful and useful. Embryology became a discipline in biology that utilized historical studies, descriptive work and experimental investigations to explore its major problems.

In considering the continuities between morphology and experimental biology, it is more accurate to depict Brooks as a transitional figure between the descriptive studies and the emergence of another branch of biological investigation, experimentation. While Brooks's own work was decidedly descriptive in character, much of it was valuable in raising important questions and in providing techniques and methods for experimentalists. This interpretation concerning the role of Brooks and morphology in the development of American biology presents an alternate view stressing the continuities between morphological studies and experimental work, thereby demonstrating that nineteenth-century morphology provided a real framework for biological science in the twentieth century.

NOTES

INTRODUCTION

1. Garland Allen, Life Science in the Twentieth Century (New York: John Wiley & Sons, 1975); William Coleman, Biology in the Nineteenth Century (New York: John Wiley & Sons, 1971); Donna Jeanne Haraway, Crystals, Fabrics and Fields (New Haven and London: Yale University Press, 1976); Erik Nordenskiöld, The History of Biology: A Survey (New York: Tudor Publishing Co., 1935); Jane Oppenheimer, Essays in the History of Embryology and Biology (Cambridge, Mass.: MIT Press, 1971). These references represent several of the major treatments of the period.

2. Personal letter from Donna Jeanne Haraway, Johns Hopkins University, Baltimore, 17 September 1976.

3. A dissertation completed recently by Roberta Jane Beeson ("Bridging the Gap: The Problem of Vertebrate Ancestry, 1859-1875." Ph.D. dissertation. Oregon State University, 1978) is one of the initial attempts to correct a similar position in studies of European morphology. Beeson supplies an excellent characterization of biological studies from 1860-1875. In particular, she develops the theme that a major aim of morphological investigations following Darwin was the search for vertebrate origins among invertebrate stock. In her study, she carefully detailed the major problems confronting these workers and the methods and techniques they used to deal with these issues.

4. Of particular interest in this regard is the growing number of young historians examining the descriptive studies. Among these are included Jane Maienschein (Dickinson College), Ron Rainger (Indiana University) and Scott Gilbert (University of Wisconsin).

5. The equally important areas of comparative anatomy and paleontology will not be of major focus in this study. As will be demonstrated in the study, embryology became the most important tool for the morphologist at the end of the nineteenth century.

6. Roberta Jane Beeson, "Bridging the Gap: The Problem of Vertebrate Ancestry, 1859-1875" (unpublished Ph.D. dissertation, Oregon State University, 1978), p. 7.

7. William Coleman, Biology in the Nineteenth Century: Problems of Form, Function, and Transformation (New York: John Wiley & Sons, 1971), p. 53-54.

8. Garland Allen, Life Sciences in the Twentieth Century (New York: John Wiley & Sons, 1975), p. 17-18.

9. Ibid., p. 25.

10. Jane Oppenheimer, Essays in the History of Embryology and Biology (Cambridge, Mass.: MIT Press, 1967), p. 154.

    Oppenheimer's position concerning the role of morphology and experimental biology is somewhat confusing. In another essay she states:

    > The customary and frequent opposition of 19th century embryology as morphological to that of 20th century as experimental is further misleading in that it accentuates the use of the experimental method as an end in itself rather than as an adjunct to the descriptive method which deals with more obvious embryonic features. (Ibid., p. 5)

    She continues by contrasting the difference between the nineteenth century and twentieth century as residing in the nature of the problems. The early work was of a single focus, that of the germ-layer theory. Departure from this in the twentieth century allowed embryologists to treat morphogenesis in a wide variety of manners. In this interpretation, Oppenheimer states that the new practices of the embryologists were not disruptive to morphological studies, but merely added new dimensions to the studies. It appears to me that this position is quite different from the viewpoint Oppenheimer appears to be adopting as indicated by the quotation in the text. This second position is in much greater harmony with the thesis of this study.

11. Erik Nordenskiöld, The History of Biology: A Survey (New York: Tudor Publishing Co., 1935).

12. Ibid., p. 573.

13. Ibid., p. 594.

14. Edmund Beecher Wilson, "The Embryological Criterion of Homology," Biological Lectures Delivered at the Marine Biological Laboratory of Wood's Hole, 1894 (Boston: Ginn & Company, 1895), p. 124.

Chapter One: State of Morphology in the United States circa 1875

The study of morphology, or the "science of forms" according to Ernst Haeckel (1834-1919),[1] was probably the most characteristic feature of biological investigations in America prior to the 1890's. The aim of this program was essentially twofold. First, as indicated by Haeckel, morphology was concerned with the descriptive investigation of the form and structure of living organisms. Work of this nature involved descriptions of the character of the adult organism (anatomy) or descriptions of the developmental stages of the organism (embryology).[2] However, the work conducted by the morphologists did not end with the descriptive studies. There was the second objective of these investigations that was essentially of a speculative or hypothetical nature. It was generally understood that morphology also involved the attempt to elucidate the ancestral relationships that existed between different organisms.

> To morphology belongs the task of pointing out the identity of plan under the most diverse conditions of organization and habits of life, not only among animals of the same group but also between those of different groups.[3]

These relationships, as most morphologists would agree, indicated the probable ancestry of the organic forms. Using this information, the morphologist could speculate upon the complete genealogical heritage of different species, genera, families, etc.

The exact nature of the morphological studies that characterized American biology in the second half of the nineteenth century was primarily influenced by two traditions. Both traditions were clearly articulated and disseminated widely in the United States by 1860 as the result of two publications. The first tradition involved the descriptive study of development that was encouraged by Louis Agassiz (1807-1873) through his work and instruction at the Museum of Comparative Zoology (MCZ) at Harvard. His views concerning morphological work were published in 1857 as "Essay on classification."[4] The second tradition was evolutionary biology originating with the publication of Charles Darwin's (1809-1882) On the Origin of Species in 1859.[5]

Louis Agassiz originally came to the United States from Europe in 1846 to provide a series of lectures to the citizens of Boston through the generosity of the Lowell Institute.[6] The lectures proved to be so popular, Agassiz was tremendously charming, and the people of Boston were so impressed that he was asked to remain in America and to accept a professorship at the Lawrence Scientific School of Harvard. Agassiz agreed to the offer and remained at Harvard for the rest of his life. As a member of the faculty he developed the major program for the study of natural history in the United States. The Museum of Comparative Zoology, the result of Agassiz's determination to found a separate institution to promote biological investigations, became the first institution to offer graduate instruction in science in the United States and the only institution offering such a program during Agassiz's lifetime. David Starr Jordan (1851-1931), a student of Agassiz who later served as the president of Stanford University, emphasized the influential nature of the MCZ by stating that in "an important sense the Museum of Comparative Zoology was the first American university."[7]

One of the most impressive indications of Agassiz's influence on the development of American biology in the last half of the nineteenth century can be obtained from an examination of his students. With very few exceptions, America's most eminent biologists following 1850 were students of Agassiz and products of the instruction at the MCZ. Included among them were Alexander Agassiz (1835-1910), J. A. Allen (1838-1921), W. K. Brooks, William H. Dall (1845-1927), Walter Faxon (1848-1920), J. Walter Fewkes (1850-1930), Samuel Garman (1843-1927), Alpheus Hyatt (1838-1902), David Starr Jordan, John L. LeConte (1825-1883), Charles S. Minot (1852-1914), Edward S. Morse (1838-1925), John McCrady (1831-1881), Alpheus S. Packard (1839-1905), Frederick W. Putnam (1839-1915), Nathaniel S. Shaler (1841-1906), Samuel H. Scudder (1837-1911), Philip R. Uhler (1835-1913), Addison E. Verrill (1839-1926), Burt G. Wilder (1841-1904) and Charles O. Whitman (1842-1910).[8] These men were all important in the establishment of initial biology programs in many American colleges and universities in the last half of the nineteenth century.

Not only did Agassiz institute the initial center for biological research in the United States, but he also established America's first marine laboratory.[9] Agassiz had become convinced that zoological research should involve more attention to embryology and take advantage of America's extensive marine habitat.[10] Obviously these studies were more conducive to a laboratory situation located on the coast.

> The limited attention thus far paid in this country to the study of Embryology has induced me to enumerate the works relating to this branch of science more fully than any others in the hope of stimulating investigations in this direction. There exists upon the continent a number of types of animals, the embryological illustration of which would add immensely to the stock of our science; . . . not to speak of the opportunities which thousands of miles of sea coast, everywhere easily accessible, afford for embryological investigations, from the borders of the Arctic to the Tropics.[11]

The work in and administrative duties of the MCZ, however, distracted Agassiz from fulfilling his desire to build a marine laboratory until the last year of his life. Then, largely due to the beneficence of John Anderson (n.d.), a wealthy New York businessman who gave the island of Penikese to Agassiz and underwrote the expenses for the seaside laboratory with Central Park bonds, the Anderson School of Natural History was opened in 1873.[12] While the school lasted only one year following Agassiz's death in December of 1873, it was to be extremely important for other marine laboratories. Many of those who attended the initial summer session on Penikese became directly involved in the proliferation of other stations. These included W. K. Brooks (Chesapeake Zoological Laboratory), Alpheus Hyatt (Annisquam Seaside Laboratory), Alexander Agassiz (Rhode Island-Newport Research Laboratory), A. S. Packard (Salem Marine Zoological Laboratory), David Starr Jordan (Hopkins Marine Laboratory), Edward S. Morse (Enoshima, Japan) and Charles O. Whitman (Lake Biology Laboratory and Marine Biological Laboratory).[13]

The influence Agassiz had upon American biology was not confined to institutional developments. While the MCZ and the

Anderson School of Natural History met a critical need in America for such institutions and spawned an interest in the formation of similar organizations, the teaching of biology was complicated by a paucity of theoretical or textual material in zoology available in English. As late as 1848, there existed no comprehensive American text in zoology. Recognizing this problem, Agassiz immediately addressed himself to the deficiency as soon as he became established in Cambridge. With A. A. Gould (1805-1866), a colleague at Harvard, Agassiz published Principles of Zoölogy in 1848.[14] The book became quite popular. It was revised in 1851 and subsequently reprinted throughout the remainder of the nineteenth century in numerous editions.[15]

Since both Agassiz and Gould realized that "No similar treatise now exists in this country" and that the only source for much of the material they included in Principles of Zoölogy was in technical articles,[16] their initial intent was to present the material in a form that could be easily understood by the beginning student.

> The design of this work is to furnish an epitome of the leading principles of the science of Zoology, as deduced from the present state of knowledge, so illustrated to be intelligible to the beginner.[17]

The "epitome" was, however, not completely unbiased in the selection of the "leading principles" that were included within the text. The preface stated clearly that the "principles of Zoology developed by Professor Agassiz . . . have been generally adopted . . ."[18] along with the results of recent investigations that augmented these principles. As a result, the zoology that the early students of natural history were exposed to through Principles of Zoölogy decidedly reflected Agassiz's own biological biases.

Prior to coming to America, Agassiz studied and taught in several of the leading universities of Europe. Through his mentors, Lorenz Oken (1779-1851) and Friedrich Wilhelm Joseph Schelling (1775-1854), Agassiz became thoroughly schooled in the German tradition of Naturphilosophie. His own interpretation of Naturphilosophie was that nature revealed evidence of a creative power and a creative plan in its design and organization. Everything in the natural world was then interpreted in terms of moving toward the perfection of the creative plan for nature. Just as Oken and Schelling were the influential figures for Agassiz's philosophical background, Ignaz Dollinger (1770-1841), a professor of anatomy at Würzburg, provided the major influence upon his practice in biology. Dollinger instilled in his students, like Karl Ernst von Baer (1792-1876), a passion for problems of developmental history.[19] This interest received further inspiration from Agassiz's association with Georges Cuvier (1769-1832) during Agassiz's stay in Paris following the completion of his doctorate.[20] The work Agassiz was to undertake at Neuchatel from 1832-1846 reflected the synthesis of these influences. Agassiz accepted Cuvier's formulation of the real existence in nature of four types of organic beings. All organized bodies could be grouped under one of the four types. Each type, in turn, was constructed after the creative design or plan in nature. Examination of the development or evolutionary history of organisms revealed to Agassiz that there was no evidence for any genetic relationship between different types. That is, each of the types had a distinct and definitive plan after which all members of that type were constructed. Any change of the organism was within the limits of the type. In fact, the developmental history of an organism exhibited change only toward the gradual perfection of the creative plan.[21]

Agassiz brought his adherence to Naturphilosophie, the doctrine of four real types in nature and an interest in the development of animal form and structure with him to America in 1846. In Principles of Zoölogy these characteristics are evident as is the intention of Agassiz and Gould to provide the guiding principles for systematic work in zoology. Stating that true or natural classification schemes must be based on the study of organ development in embryos, the text stated the following:

> After this account of the history of development of the egg, the importance of Embryology to the study of systematic Zoology cannot be questioned. For evidently, if the formation of the organs in the embryos takes place in an order corresponding to their importance, this succession must in itself furnish a criterion of their relative value in classification. Thus, those peculiarities that first appear should be considered of higher value than those that appear later. In this respect, the division of the Animal Kingdom into four types, the Vertebrates, the Articulates, the Mollusks, and the Radiates, corresponds perfectly with the gradations displayed by Embryology.[22]

Embryology, therefore, became the most important tool for classification work. The study of zoology was encouraged to examine organisms in their developmental stages to determine the organism's relative position within its type. While Agassiz was not advocating any genetic evolutionary relationship between closely related organic beings, he did believe that nature provided a gradation of organic forms within each type.

Systematic zoology, following the guidelines put forward in Principles of Zoölogy, necessarily involved the question of the precedence of animals within a type. To examine the relative position of an organism, the natural historian became involved in distinguishing between homological features and analogical features in the organisms under consideration.[23]

> Affinity or homology is the relation between organs or parts of a body which are constructed on the same plan, however much they vary in form, or even serve for very different uses. Analogy, on the contrary, indicates the similarity of purposes or functions performed by organs of different structure.[24]

Homologies were, by definition, restricted to organisms constructed upon the same plan or within the same type. Therefore, homological structures could be used to determine the systematic position of organisms. Structures that were closely homologous indicated a close relative position within the type. Structures that lacked such an immediate homology were more distantly related. Analogical relationships were used to describe similarities existing between different types. This relation was not due to form, but was due to the purpose or function of the structure. Relations of purpose or function had no bearing upon systematic relatedness. Furthermore, since analogies existed between different types, by definition they were unimportant for determining the precedence of organic beings. It was studies of homologies and analogies that became a hallmark of investigations carried out by Agassiz's students at the MCZ and, later in the nineteenth century, by many American morphologists.[25]

Agassiz's clearest and most influential exposition concerning systematic zoology was published in 1857 as the "Essay on classification."[26] It was in this work that many of the ideas sketched out in preliminary form in Principles of Zoölogy were fully expanded to their mature form. Additionally, Agassiz wanted to present a general treatise concerning the most recent developments in embryology. Citing Karl Ernst von Baer's discovery of the universal presence of eggs in all animals as the greatest discovery in natural science,[27] Agassiz noted that embryology had subsequently developed into the most important branch of natural history. Extensive investigations into the manner of differentiation of organisms from an homogenous mass led to studies of the phenomena of development in as many animals belonging to as many different types as possible. "Essay on classification" was the first general work to address itself to this research.[28] It was Agassiz's aim that such a presentation would provide the foundation upon which the natural system of classification could be established.

> It has appeared to me appropriate therefore to present here a short exposition of the leading features of the animal kingdom, as an introduction to the study of Natural History in general and of Embryology in particular, as it would allow a desireable opportunity of establishing a standard of comparison between the changes animals undergo during their growth, and the permanent characters of full-grown individuals of other types, and perhaps of showing also what other points beside structure might with advantage be considered in ascertaining the manifold relations of animals to one another and to the world in which they live, upon which the natural system may be founded.[29]

These remarks provide the general character of the work.

According to Agassiz, the four types that existed in nature were as follows: Radiata, which included the groups Polypi, Acalephae and Echinodermata; Mollusca, which was subdivided into Bryozoa, Brachiopoda, Tunicata, Cephalopoda, Lamellibrachiata and Gastropoda; Articulata, which consisted of Vermes, Crustacea and Insects; and Vertebrata, the most advanced type.[30] The "Essay on classification" was not restricted to a mere catalog of the successive development of specific organisms belonging to each type. Instead, Agassiz's goal was much more ambitious.

> Embryology has, however, a wider scope than to trace the growth of individual animals, the gradual building up of their body, the formation of their organs, and all the changes they undergo in their structure and in their form; it ought also to embrace a comparison of these forms and the successive steps of these changes between all the types of the animal kingdom, in order to furnish definite standards of their relative standing, of their affinities, of the correspondence of their organs in all their parts . . . . there remains a wide field of investigation to ascertain the different degrees of similarity between the successive forms an animal assumes until it has completed its growth and the various forms of different kinds of full-grown animals of the same type; between the different stages of complication of their structure in general and the perfect structure of their kindred; between the successive steps in the formation of all their parts and the various degrees of perfection of all the parts of other groups; between the normal course of the whole development of one type compared with that of other types, as well as between the ultimate histological differences which all exhibit within certain limits.
>
> I satisfied myself long ago that Embryology furnishes the most trustworthy standard to determine the relative rank among animals.[31]

The study of development, therefore, became the most important tool for those who were to follow the program of Agassiz.

While the major goal for embryology was to determine the "relative rank among animals" Agassiz was also looking for corroborative evidence for his acceptance of the Cuvierian doctrine of four types. The two major questions addressed in "Essay on classification" were, "Do all animals form one unbroken series from the lowest to the highest?"[32] and "Does the animal kingdom constitute several or any number of graduated series?"[33] Embryological investigations upon the first question substantiated Cuvier's work in that it indicated animals do not form an unbroken series from the lowest forms to the most complex organisms. Of the four types, it was true that there was increasing complexity from the Radiata to Mollusca to Articulata to Vertebrata. However, each type was genetically unique and, furthermore, constructed according to a completely autonomous plan. There were absolutely no grounds upon which one could consider any gradual or actual relatedness between types.

Agassiz offered similar embryological arguments to support the view that there were graduated series of organisms in the animal kingdom, but that the number of series was restricted to the number of types, four. Each type illustrated within itself a graded series from the simple to the more complex. However, this gradation did not indicate genetic connection between the organisms in the type. Instead, the gradation only revealed the idea of the Creator to construct organisms according to four specific plans in nature.[34]

In reflecting upon the serial relationships of related organisms, Agassiz considered the relationship between ontological developments and the phylogenetic position or ranking of the organism within the type. Agassiz felt that there was a relation between the embryonic growth of organisms and the organism's "succession in time."[35] Following the example of Johannes Müller's (1801-1858) work on echinoderms,[36] Agassiz conducted embryological investigations upon Acaphalae, Gastropoda, Lamellibranchiata, Cephalopoda and Brachiopoda. The results of his work justified this relationship.

> . . . that while the young Lamellibranchiata are still in their embryonic stage of growth, they resemble, externally at least, Brachiopods more than their own parents, and the young shells of all Gasteropods known in their embryonic stage of growth, being all holostomate, recall the oldest type of that class.[37]

Work on crustaceans added further evidence for the view of a correlation between geological succession and embryological change. The evidence was sufficient to conclude that,

> . . . enough has already been said to show that the leading thought which runs through the succession of all organized beings in past ages is manifested again in new combinations, in the phases of the development of the living representatives of these different types.[38]

Agassiz was quick to point out, however, that the correspondence between gradation within the type and embryonic change did not necessitate any genetic connection. It only provided additional support for evidence of a "plan designed by an intelligent Creator."[39]

Agassiz also argued for a careful evaluation of embryological changes that appeared to indicate that development was a progressive movement from generalized forms to more specific forms. Since this idea, especially in the form of the work of von Baer, could conceivably support the idea that all four types shared a common generalized form (i.e., an homogeneous and homologous egg), Agassiz took exception to it. He stated that the entire notion was extremely problematic since there did not exist any general agreement concerning which embryonic characteristics were general and which were specific.[40] He maintained, instead, that as soon as the process of differentiation began, the investigator could immediately observe distinguishing characteristics of the type.

> As eggs, in their primitive condition, animals do not differ one from another; but as soon as the embryo has begun to show any characteristic features it presents such peculiarities as distinguish its type. It cannot therefore be said that any animal passes through phases of development, which are not included within the limits of its own type; no Vertebrate is or resembles, at any time, an Articulate, no Articulate a Mollusk, no Mollusk a Radiate, and *vice versa*.[41]

Progressive developmental changes could be compared, but homological changes were exhibited within the type.

The importance of homological versus analogical structures in classification was afforded a similar position of importance in the "Essay on classification" as it was in *Principles of Zoölogy*. Again, it was the embryological investigation of these relationships that was most important for Agassiz.[42] In particular, embryological studies revealed that studies of homology, or true affinity, provided a real criterion for the relatedness of organisms since homologies were restricted to members of the same type.

> Embryology affords further a test for homologies in contra-distinction of analogies. It shows that true homologies are limited respectively within the natural boundaries of the great branches of the animal kingdom.[43]

In some instances, this information provided the investigator with the initial indication of the affinity between organisms while in other cases it provided the confirmation of such an affinity that had been previously suggested but not established.[44]

The emphasis that Agassiz placed upon the study of embryology to determine the natural relationships of organisms exerted a strong influence upon the character of the research conducted at the MCZ. While he stated that embryological work in systematics needed to be fortified by studies of anatomical similarities between animals and the study of the paleontological record of the organisms, it was quite clear that the morphological relationships were most clearly established upon developmental grounds.[45] As a result, many of the most characteristic and most impressive studies of the period prior to 1875 in America dealt with embryology. John McCrady investigated the developmental history of acalephs; Edward Desor (1811-1882) and Charles Girard (1822-1895), Agassiz's collaborators, worked on the embryology of various worms; Alexander Agassiz, Louis's son and eventual successor as the director of the MCZ in 1873, published influential papers on the embryology of echinoderms (1864, 1874), annelids (1866, 1873) and ctenophores (1874); Jeffries Wyman (1814-1874), an instructor at the MCZ, wrote a paper on the developmental stages of the skate; Alpheus Hyatt, later to be one of the main forces in the American neo-Lamarckian community, worked on the embryology of several ammonites; Edward S. Morse, another neo-Lamarckian, published several works on the early stages of Terebratulina (1869-1873), an important brachiopod, that eventually precipitated a major revision in Agassiz's taxonomy by forcing the move of Brachiopoda from a sub-division of Mollusca to a position in closer proximity to Annelida; and Alpheus S. Packard, the third member of the American neo-Lamarckian group,[46] investigated the development of _Limulus_.[47]

The studies conducted at the MCZ helped to provide the American biology community with a good foundation in embryological work. Alpheus Packard noted this character.

> We may, then take an honest pride in the embryological work done by American students; for in this department great activity was shown when scarcely anything was being done in England or France, and the United States have been for twenty-five years past second in embryology studies to Germany, the mother of developmental zoology.[48]

Studies of the structure and development of organic beings became such a dominant activity of biological studies in America that Wesley Coe (1869-1960) characterized the period of 1847-1870 as the "Period of morphology and embryology."[49]

The science that Agassiz practiced exerted an influence not only over the character of the studies, but also over the educational regime for students in natural history. In addition to an exposure to his own theoretical views and practical methodology, Agassiz made available to the students the ideals and methods of the European zoological community. He maintained an active interest in the developments taking place in Europe and communicated extensively with many of the major European morphologists. While later generations of biologists would seek to go to Europe to work in the more experimental laboratories, Agassiz's students were content to enjoy the preparation available to them.

> It did not seem necessary to go to Germany, for we were enjoying advantages equal to those of the best German laboratories.[50]

After 1859, the supremacy of Agassiz's typological arrangement for systematics was challenged. However, as one of his students accurately pointed out, the character of the biology Agassiz practiced may have contributed to the challenge.

> The facts may be of the same general nature, but their interpretation has radically changed; and it is fair to say that the labors of Agassiz in embryology and paleontology had some influence in leading to this change.[51]

Of greater influence for the shift in interpretation was the second tradition that influenced the late nineteenth-century morphological studies. Shortly after the publication of Agassiz's "Essay on classification" in 1857, Charles Darwin published his monumental work, On the Origin of Species in 1859. This work affected the character of subsequent developments in nineteenth-century biology as no other work published in the century. Darwin's impact upon morphology was equally impressive.

Before the Origin was published, there were two primary interpretations concerning the study of forms. The distinction between the two is subtle for both are based upon the idealistic conception of forms. Organic beings were depicted either as expressing a creative plan in nature or forms were seen as indicating the existence of a purely Platonic or archetypal idea in nature.[52] Louis Agassiz reflected the closeness of these conceptions by utilizing both viewpoints. While forms of different organisms might appear to resemble one another, the similarity was only due to the fact that organisms of the same type had been constructed upon a similar plan or according to an universal idea. Any similitude did not connote real organic relationship; indeed, only identical forms were related, others presented absolutely no genetic link. As a result, pre-Darwinian morphology had as its goal the aim to discover and work out in detail the unity of plan underlying the diversity of forms, to disentangle the constant element in animal form and to distinguish the essential animal form from the necessary or adaptive forms.[53] The principal method was to compare adult structures or to undertake a comparative study of developing embryos. Comparative anatomy of adults was the preferred method in the early part of the nineteenth century, but later investigations (after mid-century), such as the work of Agassiz, switched to embryological studies.

After the Origin was published, the interpretation of form changed dramatically. A more dynamic view of organisms was accepted to replace the static type concept based upon the ideal nature of forms. This new conception included the actual genetic relatedness of organic beings due to common descent through modification.

> The needful solution was effected by Darwin. The "urpflanze" of Goethe, the types of Cuvier, and the like, at one became intelligible as schematic representations of ancestral organisms, which, in various and varying environments, have undergone differentiation into the vast multitude of existing forms. All the enigmas of structure become resolved; "representative" and "aberrant," "progressive" and "degraded," "synthetic" and "isolated," "persistent" and "prophetic" types no longer baffle comprehension; conformity to type represented by differentiated or rudimentary organs in one organism is no longer contradicted by their entire disappearance in its near allies, while systematist and morphologist become related simply as specialist and generalizer, all through this escape from the Linnaean dogma of fixity of species. The phenomena of individual development receive interpretation in terms of ancestral history; and embryology thus becomes divided into ontogeny and phylogeny, while classification seeks henceforth the reconstruction of the genealogical tree. All these results were clearly developed in the most important work of the new period. [Origin of Species][54]

By stressing the genetic connections between species, Darwin laid the foundation for evolutionary morphology. Instead of explaining homological parts as representing the unity of plan or perfect adaptation by a creative being or offering a teleological explanation, animals became understood as forms descended one from another. In this manner, Darwin addressed the main problems of pre-evolutionary morphology; the natural classification scheme was actually genealogical; systematic relationships actually represented genetic relationships; homology and analogy became interpreted in terms of heredity and adaptation; the unity of plan was defined as descent from a common ancestor; and "ancestral form" became substituted for archetype.[55]

Darwin's unity of descent was dependent upon his assumption that organisms exhibited variation of form and structure in nature. In fact, Darwin understood variation to be an exhibited fact of natural history. It was this inherent trait of all organisms that allowed them to respond to varying conditions in the external environment. Variation, in turn, was acted upon by natural selection. It was natural selection that acted to determine which variations would survive and reproduce and which variations would be eliminated. The final result of this process, in simplistic terms, was that natural selection acting upon variation over a long period of time could give rise to speciation. It was in this manner that Darwin sought to explain the unity of descent.

One of the most critical elements of Darwin's theory was that variation was characteristic of the genetic material. That is, whatever the hereditary units were that passed from the parental stock to the offspring, they exhibited an unique tendency to vary in nature. Since variation was limited to speciation, after 1859 the problems of heredity and variation became inseparable from discussions of the cause of phylogeny.[56] Evolutionary morphologists insisted on providing an hereditary scheme that provided a plausible explanation of phyletic development. Ontogeny, or embryonic development, became the common tool to explain the process.

As mentioned above, Darwin believed all organisms had a genetic relationship as the result of gradual descent from a common ancestor. Stating the problems associated with founding a natural system on the premise that such a system reflected the plan of a Creator,[57] Darwin concluded;

> All the foregoing rules and aids and difficulties in classification are explained, if I do not greatly deceive myself, on the view that the natural system is founded on descent with modification; that the characters which naturalists consider as showing true affinity between any two or more species, are those which have been inherited from a common parent, and, in so far, all true classification is genealogical; that the community of descent is the hidden bond which naturalists have been unconsciously seeking, and not some unknown plan of creation, or the enuciation of general propositions, and the mere putting together and separating objects more or less alike.[58]

Darwin took care to emphasize that the arrangement of species must be genealogical in order for the classification scheme to be a natural one. In terms of classification, therefore, the modifications from a common ancestor would be expressed by the various rankings on the genealogical "tree."[59] It was the task of the naturalist to determine the position of the various organisms on such a classification scheme and to determine which characteristics should be most important for the relative ranking.

To investigate problems of classification or descent, Darwin felt morphology was the best prepared tool since it included the study of the resemblance of members of the same taxonomic unit.[60] In fact, morphology for Darwin was "the most interesting department of natural history, and may be said to be its very soul."[61] While morphology was further divided into the study of adult forms and embryonic forms, Darwin felt that investigations of the embryo provided the most information for evidence concerning the unity of descent.

> Descent being on my view the hidden bond of connexion which naturalists have been seeking under the term of the natural system. On this view we can understand how it is that, in the eyes of most naturalists, the structure of the embryo is even more important for classification than that of the adult, for the embryo is the animal in its less modified state; and in so far it reveals the structure of its progenitor. In two groups of animals, however much they may at present differ from each other in structure and habits, if they pass through the same or similar embryonic stages, we may feel assured that they have both descended from the same or nearly similar parents and are therefore in that degree closely related. Thus, community in embryonic structure reveals community of descent.[62]

Not only did embryology provide corroborative evidence for the unified ancestry of organisms, but Darwin's theory of the descent of species was in harmony with many of the facts of embryology.

> Thus, as it seems to me, the leading facts in embryology, which are second in importance to none in natural history, are explained on the principle of slight modifications not appearing, in the many descendants from some one ancient progenitor, at a very early period in the life of each, though perhaps caused at the earliest, and being inherited at a corresponding not early period. Embryology rises greatly in interest, when we thus look at the embryo as a picture, more or less obscured, of the common parent-form of each great class of animals.[63]

Darwin was convinced that embryological information provided the essential basis to substantiate the community of descent since the "embryo comes to be left as a sort of picture, preserved by nature, of the ancient and less modified condition of each animal."[64]

Darwin's emphasis upon the unity of descent was mirrored in several of his subsequent works to the Origin. In The Variation of Animals and Plants under Domestication (1868), he stated that his theory that "members of the same order or class . . . are descended from a common progenitor" was generally accepted by "our best naturalists . . ."[65] In The Descent of Man (1871), Darwin once again argued against a teleological interpretation of homologous structures, by offering a "scientific explanation."

> With respect to development, we can clearly understand, on the principle of variations supervening at a rather late embryonic period, and being inherited at a corresponding period, how it is that the embryos of wonderfully different forms should still retain, more or less perfectly, the structure of their common progenitor. No other explanation has ever been given of the marvellous fact that the embryos of a man, dog, seal, bat, reptile, etc., can at first hardly be distinguished from each other.[66]

In this manner, Darwin continued to advocate ontogenetic studies for their application to systematics throughout his lifetime.

The interest in the contribution that studies of ontogeny could make to genealogies prompted T. H. Huxley (1825-1895), Darwin's leading defender and popularizer in the mid-nineteenth century, to state that by formulating evolutionary morphology Darwin introduced a new element into taxonomy.

> If a species, like an individual, is the product of a process of development, its mode of evolution must be taken into account in determining its likeness or unlikeness to other species; and

> thus "phylogeny" becomes not less important than embryology to the taxonomist.[67]

Indeed, phylogenetic considerations became a major focal point for not only taxonomists, but for anyone working on anatomical, embryological or paleontological investigations. The real difference between these studies conducted under a Darwinian interpretation and similar studies conducted under the guidance of Louis Agassiz, was that no longer were embryonic similarities considered to be illustrative of homologies existing only within the confines of one type. Homologous structures were now considered to indicate propinquity of descent; that is closely homologous organisms shared a close ancestral heritage. As a result, investigations of homologies between organisms revealed the actual evolutionary pattern of organisms, not just the adherence of organisms to creative types.

The change from the fixed species or type concept of Agassiz to a dynamic or mutable species concept advocated by Charles Darwin provided the essential difference between these two programs for those involved in morphological studies. In spite of the apparent magnitude of the nature of such a switch, the actual practices and methods of biological investigation did not change significantly. The basic research areas remained the same, with most attention directed toward embryological work while comparative anatomy and paleontology served lesser but still very important roles. From the previous discussion, it is apparent that both Agassiz and Darwin viewed studies of development as providing the best information for taxonomic questions. Therefore, the role of the embryo in such studies remained basically unchanged and the work discussing homologous and analogous structures continued. The only difference was that homologies were no longer discussed as being restricted to one type. Instead, any organ that had a common embryonic history between two or more organisms, regardless of the taxa of the organisms under consideration, could possibly be homologous. Analogies continued to have the same lesser value for discussions of ancestry as did homologies. Darwin referred to such structures as having an "adaptive character, although of the utmost importance to the welfare of the being, are almost valueless to the systematist."[68] The emphasis upon homological relations that was begun by Agassiz, therefore, remained under the Darwinian approach.

Since Darwin recognized morphology as being most concerned with the study of types and homologies,[69] investigations of this nature characterized the last half of the nineteenth century. In particular, since homologous structures were directly related to the common inheritance of characters from a shared ancestor, these provided valuable information for studies of probable descent. Obviously the connection between these studies and evolution was very intimate. This relationship is strongly supported by the work that was completed under the Darwinian influence. In 1867, Alpheus Hyatt published his evolutionary work, "On the parallelism between the different stages of life in the individual and those in the entire group of the molluscous order, Tetrabranchiata." Similar studies were undertaken by Edward Drinker Cope (1840-1897); in 1868 he published, "Origin of genera" and in 1871, "On the method of creation of organic types." Other works, instead of investigating and describing only the developmental stages of organisms as was commonplace under Agassiz, looked increasingly upon the developmental history of organisms in terms of the probable lines of species descent. Some notable examples of this work include investigations by Alpheus Hyatt on the probable ancestry of cephelapods, by A. S. Packard on the descent of insects and by Edward S. Morse on the evolutionary relationships of brachiopods.[70] The investigations of similar topics became so pervasive that Wesley Coe labeled the years from 1870-1890 as the "period of evolution."[71] Studies in morphology dominated biological work, reaching the apex toward the end of the nineteenth century under the guidance of C. O. Whitman, E. L. Mark (1847- ?), Charles S. Minot, W. K. Brooks, J. S. Kingsley (1854-1929) and E. B. Wilson.

> The morphological, embryological and paleontological evidences of evolution as indicated by homologies, developmental stages and adaptations were the most absorbing subjects of zoological research and discussion.[72]

It should be emphasized that the genealogical work conducted under the aegis of the Origin of Species did not necessitate a complete break from the influence of Louis Agassiz. In fact, in a real sense the work following 1859 can be most accurately interpreted as a product of the influence of both Agassiz and Darwin. Certainly both emphasized the need for morphological studies to investigate the relatedness for forms. Both utilized research in comparative anatomy, embryology and paleontology. And, both Darwin and Agassiz stressed the importance that embryological work involving the early developmental history could have upon questions of classification. To illustrate further the compatible nature of the two approaches, it is interesting to note that the majority of the leading American biologists after 1850 were educated under Louis Agassiz. Yet, in less than a decade following the publication of the Origin, all had shifted from the fixed species concept to the evolutionary program of Darwin. Several of these men felt that the educational program of Agassiz facilitated the acceptance of Darwinian evolution theory.

> In this respect Agassiz did not rise above the limitations of his time and his own nature, but the facts he worked out, or which his students and collaborators discovered, were freely given to his students and in this respect if he did not grasp, or was unwilling to accept, the conclusions of Lamarck and of Darwin, he paved the way for the adoption by his students of evolutional views.[73]

The author of this passage, A. S. Packard, also stated his belief that he thought Agassiz had a greater sympathy for evolution than he has been traditionally credited with. Following a lecture Packard had given demonstrating the probable genetic relationship between Limulus and other arthropods, Agassiz responded to him by stating:

> I should have been a great fellow for evolution if it had not been for the breaks in the paleontological record.[74]

Indeed, Agassiz's opposition to evolution in general and Darwin's program in particular was not based upon the same weak grounds as much of the opposition from others.[75] He, at least, always entertained opposing views to the type theory, if only in a pedagogic sense. His students were well informed as to the status of the prevailing views on evolution and were encouraged to evaluate the various theories.

The essential change in biological studies, therefore, was restricted to the abandonment of the early nineteenth-century concept of fixed types existing in nature. As E. S. Russell (1887-) stated, Darwin provided the needed solution to the main problems of pre-evolutionary morphology.[76] Before Darwin, Agassiz and his students were investigating natural classification systems, the systematic relatedness of organisms with apparently similar forms and reasons for the existence of homological and analogical structures. However, it was not until after 1859 that an alternative to fixed species was clearly offered. Henceforth one could legitimately entertain the possibility that organisms shared common structures and belonged to similar natural taxonomic units because they shared a common ancestral heritage. Still the methods employed in morphology remained basically the same.

> In what follows we shall see that the coming of evolution made surprisingly little difference to morphology, that the same methods were consciously or unconsciously followed, the same mental attitudes taken up, after as before the publication of the Origin of Species.[77]

In a real sense, therefore, it is accurate to state that morphology in the second half of the nineteenth century did not undergo a major change after Darwin's work. Instead it bears the dual imprint in the United States of both Agassiz and Darwin.

In spite of the fact that morphological practices in America did not change dramatically after Darwin, the impact of the theory of the descent of species upon morphology should not be minimized. It was only after the publication of the Origin of Species that morphological work came to be characterized by its genealogical nature. Evolution provided morphology with the conception of the organism as an historical being. As a result, it became commonplace to present the historical interpretation of animal structures.[78] Pure morphology became the practice of looking beyond the diversity of organic forms for the underlying unity throughout all organic beings.

While Darwin had a marked influence upon the character of morphological studies, this influence should not be interpreted as indicating that Darwin's conception of evolution was universally accepted in its entirety. In fact, in the United States the opposition to certain points was vocal. However, the major problems with Darwin's views mainly concerned the mechanisms that explained evolutionary change. That evolution, or the descent of species by modification from a common ancestor or ancestors, had occurred was accepted by virtually the entire biological community. This acceptance and the realization of the importance of evolution for biology was recognized and commented on by several major figures from the late nineteenth century. In an article printed in the Annual Report of the Smithsonian Institution, 1900, the German biologist Oscar Hertwig (1849-1922) proclaimed:

> For we may say, with Huxley, "If the Darwinian hypothesis were swept away, evolution would still stand where it was." In it we possess a permanent acquisition of our century; one of its greatest, and resting upon facts.[79]

This view was echoed by the American, E. G. Conklin (1863-1952), who called Darwin's doctrine of organic evolution the "greatest scientific generalization of the past century."[80]

> There have been, of course, assertions which outran evidence, and skepticism which denied all evidence, but in spite of these excesses every year since 1859 has contributed in ever increasing measure to the complete establishment of the doctrine of descent and to the wider extension of this theory into every field of human thought and endeavor.[81]

Many of the biologists working on morphological questions in America shared Hertwig's and Conklin's attitude toward the impact Darwin had upon biology. At the same time, many of these workers either chose to ignore, at least temporarily, the problems with the mechanism for evolution, or to accept tentatively Darwin's theory of natural selection, or to postulate additional mechanisms to explain the various phenomena associated with evolution theory.

Whatever attitude was taken concerning evolution, the primary aim of the studies was to uncover the relations that existed between various organic forms. Such investigations were undertaken in basically three ways.[82] One method was to determine the basic unity of plan underlying the diversity of form. Another effort was directed toward discovering a common ancestor or archetype for divergent groups. A third approach was to reconstruct the phylogenetic history of a group of organisms. All of these approaches to systematic zoology provide evidence for the displacement of the type concept in favor of a more evolutionary concept of species descent.

As previously mentioned, much of the work in the American biological community prior to 1875 illustrated the concern for questions of a genealogical or evolutionary nature. However, it is difficult to identify the work of the community with any real institution of American biologists. Quite simply, there was a paucity of such groups. The only institution that actually existed for biological instruction was the Museum of Comparative Zoology at Harvard. The importance of the impact of this institution on the character of late nineteenth-century biology has been previously documented. In addition to the MCZ, the Boston Society of Natural History served as a gathering place for those interested in natural as well as offering periodic instruction upon biological topics. Perhaps more importantly, it offered a few professional positions for practicing biological investigators. Probably the only other influential center of biological work was centered in Salem, Massachusetts. It was here that the Essex Institute (later the Peabody Academy of Science) was located. This became the major neo-Lamarckian institution in the 1870's with A. S. Packard, Edward S. Morse and Alpheus Hyatt making significant contributions.

In terms of biological journals, the offerings were about as scarce as the institutions. The Boston Society of Natural History began publishing a journal in 1837 and the Proceedings in the 1840's. But the more important Memoirs was not begun until 1866. The MCZ published both a Bulletin and a Memoirs, the earliest dating from 1863. None of these publications, however, was dedicated to publishing articles of a strict zoological nature. The American Journal of Conchology, a journal dedicated to the systematics of molluscs issued beginning in 1865, was the first publication aimed at a specialized field. The American Naturalist, published by Packard, Morse, Hyatt and Putnam in 1867, was the first journal of a strictly biological nature. Other major scientific journals containing material from the American biological community, such as Science (1883), Journal of Heredity (1885) and Journal of Morphology (1887), were not issued until the 1880's.

The paucity of American institutions and journals specializing in biological research prior to 1875 makes it an extremely difficult and hazardous task to attempt to identify any community of American biologists. Nevertheless, if one considers Brooks, Hyatt, Jordan, Minot, Morse, McCrady, Packard, Uhler, Verrill, Whitman and Wilder, as representing the major thrust of American biology between 1860-1875, a strong case can be made for identifying a loose "community" surrounding Agassiz and the MCZ. By examining the character of the work of these men, one can indeed see that the dominant theme of all their work was the use of comparative anatomy, embryology and paleontology for the collection of genealogical information.

In spite of the small number of formal institutions or journals, the work of the American community was not accomplished in complete isolation. There were other sources of influence on the biological work in addition to Agassiz's "Essay on classification" and Darwin's Origin of Species. Most of these works were European, for the situation facing Agassiz in 1846 concerning the lack of American textual material in zoology had not been ameliorated by the American biological community. In fact, Agassiz's Principles of Zoölogy was still the only American zoological textbook available as of 1875.[83] In this regard, the works published in Europe helped to fill the void. The problem with these sources, of course, was that the majority of the morphology texts were printed in German and few, if any, translations into English were immediately available.

Despite the language difficulties, there were several of these works that became available to the American audience. Among these were several treatises written by Alexander Kowalewsky (Aleksandr Onufrievich Kovalevskii, 1840-1901). Kowalewsky's most important work was published in St. Petersburg in the 1860's as a series of articles, Beiträge zur Anatomie und Entwickelungsgeschichte des Loxosoma neapolitanum, sp. n. (1866), Entwickelungsgeschichte der einfachen Ascidien (1866), Entwickelungesgeschichte des Amphioxus lanceolatis (1866), Beiträge zur Entwickelungsgeschichte der Holothurien (1867) and Embryologische Studien an Würmen und Anthropoden (1869). The two main themes of Kowalewsky's research became influential throughout Europe and the United States due to their application to the question of the relationship between invertebrates and vertebrates. First, he found that the larval stages or early embryonic stages of selected individuals from different phyla (chordates, chaetognaths, phoronids, echinoderms[84]) shared the common characteristic of passing through the same two-layered sac-like embryo or gastrula.[85] This work proved important to Ernst Haeckel's Gastrae theory (discussed below) and was cited in his book, The Evolution of Man (1874).

> Recently Kowalewsky and Ray Lankester especially have tried to show that other Invertebrate animals of the most diverse classes, in worms, Soft-bodied Animals (Mollusca), Star-animals (Echinoderma), and Articulated animals (Arthropoda), form from the same two primary germ layers.[86]

Second, Kowalewsky suggested that it was possible to perceive a direct evolutionary relation between vertebrates and ascidians (urochordates) by assuming that the line of evolution from the ascidians to the vertebrates involved the larval form of the ascidian. The evidence for this assumption was in the form of embryological similarities between Amphioxus chorda, considered to be a primitive vertebrate, and the axial cylinder in the larval ascidian. The axial cylinder in both organisms had the same embryological origin. It was postulated that the vertebrate line passed through a form similar to the larval ascidian, while the ascidian line branched in a separate direction. Studies in this mold provided evolutionists with a new model for vertebrate development through the invertebrate line and demonstrated the value of embryological information in determining morphological relations.[87] The importance of this work was recognized by Darwin. Giving reference to Kowalewsky's work on vertebrate ancestry, he wrote in The Descent of Man:

> Thus, if we may rely on embryology, ever the safest guide in classification, it seems that we have at last gained a clue to the source whence the Vertebrata were derived. We should then be justified in believing that at an extremely remote period a group of animals existed, resembling in many respects the

> larvae of our present Ascidians, which diverged into two great branches--the one retrograding in development and producing the present class of Ascidians, the other rising to the crown and summit of the animal kingdom by giving birth to the Vertebrata.[88]

A second source of information came through the work of Ernst Heinrich Philipp August Haeckel (1834-1919). His Generelle Morphologie der Organismen (1866) was one of the earliest morphological treatises with a strict Darwinian interpretation. This was followed by Natürliche Schöpfungsgeschichte (1868) which contained the results of Kowalewsky's research into vertebrate ancestry. Neither of these works was immediately available in English form in the 1860's. Later, however, the essential ideas of both were published in English editions entitled The Evolution of Man; A Popular Exposition of the Principal Points of Human Ontogeny and Phylogeny (1874) and The History of Creation: Or, The Development of the Earth and its Inhabitants by the Action of Natural Causes. A Popular Exposition of the Doctrine of Evolution in General, and of that of Darwin, Goethe and Lamarck in Particular (1876). Haeckel shared the view of Darwin that higher animals, including man, probably originated through some lower organic form.

> All my readers know of the very important scientific movement which Charles Darwin caused fifteen years ago, by his book on the Origin of Species. The most important direct consequence of this work, which marks a fresh epoch, has been to cause new inquiries to be made into the origin of the human race, which have proved the natural evolution of man through lower animal forms.[89]

Haeckel went on to state the exact nature of this ancestry, a view he first proposed in Natürliche Schöpfungsgeschechte in 1868. The debt to the work of Kowalewsky is clear.

> For it is now evident that the Amphioxus as the representative of Vertebrates, and the Ascidian as the representative of Invertebrates, form the bridge which alone can span the deep gulf between these two main divisions of the animal kingdom. The fundamental agreement exhibited by the Lancelot and the Ascidian in the first and the most important points of their embryonic development does not only testify their close anatomical form-relationship and their connection in the system; it also testifies their true blood-relationship and their common origin from one and the same parent form; and hence it at the same time throws a flood of light upon the earliest origin of human genealogy.[90]

To support the relationship between the main divisions of the animal kingdom, Haeckel applied the Gastrae theory in which he attempted to demonstrate that the two primary germ layers of all metazoans were homologous. Haeckel believed that all fertilized eggs developed into a gastrula form by the inversion of the blastula. When the gastrula was formed, there resulted two primary germ layers from which the same fundamental organs and tissues arose in all animals. This demonstration, Haeckel was convinced, proved the unity of descent from a primitive gastrula-like ancestor.

> Man and all those animals, which in the first stages of their individual evolution pass through a two-layered structural stage or a Gastrula-form, must have descended from a primeval, single parent-form, the whole body of which consisted throughout life, as now in the case of the lowest Plant-animals, only of two different cell-strata or germ layers.[91]

In putting forth these views, Haeckel encouraged more research to investigate his claims. Specifically, he encouraged more attention to comparative anatomy, to studies of early developmental stages and to studies of lower animal forms. Much of this work was intended to obtain more information concerning homologies. With the

Gastrae theory, for Haeckel the main criterion for homology was the similarity of development from identical germ layers.[92]

A third major source of influence was the work of Carl Gegenbaur (1826-1903). An early adherent to the views of Darwin, Gegenbaur published Grundzüge der Vergleichenden Anatomie (1859, second revised edition in 1870). The revised second edition presented a special plea for investigators in comparative anatomy to leave the static type concept and to accept Darwin's descent theory. Gegenbaur also emphasized in the later edition the results of Kowalewsky's research on vertebrate ancestry. The result of his compilation of this work and subsequent works on primitive vertebrates was a much more concrete explanation for the ancestry of vertebrates than offered by Ernst Haeckel in 1868.[93] In Grundzüge, Gegenbaur provided more empirical data to the tunicate theory of vertebrate descent through anatomical and embryological information of Amphioxus and additional homologies between ascidians and vertebrates. In this manner he served to broaden the theory in terms of additional empirical evidence.

While two editions of Grundzüge were available prior to 1875, an English edition did not appear until 1878. Nevertheless, the publication of Elements of Comparative Anatomy, translated by F. Jeffrey Bell (1855-1924) and E. Ray Lankester (1847-1929), provided the first modern work in comparative anatomy available in the nineteenth century.[94] Early in the text, Gegenbaur stated that it was the business of comparative anatomy to follow the changes in organic form and to discover the similarities that exist among these changes. Accepting Haeckel's Gastrae theory, he believed that careful investigations could reveal similarities due to the common descent from primitive germ layers. As a result, much of Gegenbaur's work emphasized the application of homological research.

> Homology therefore corresponds to the hypothetical genetic relationship. In the more or less clear homology, we have the expression of the more or less intimate degree of relationship.[95]

Nevertheless, despite the tools available to the researcher from embryological data, sometimes the genealogical situation was so obscure that the application of speculation was required.

> Not only is the student thus taught to retain and accumulate his facts in relation to definite problems which are actually exercising the ingenuity of investigators, but he is encouraged, and to a certain extent trained, in the healthy use of his speculative faculties; in fact the one great method by which new knowledge is attained, whether of little things or big things--the method of observation (or experiment), directed by speculation--becomes the conscious and distinctive characteristic of his mental activity. Thus we may claim for the study of Comparative Anatomy, as set forth in the present work, the power of developing what is called "common sense" into the more precisely fixed "scientific habit" of mind.[96]

The use of speculation was often necessary for the comparative anatomist since evidence of homological relations between organic forms was often obscured due to evolutionary modifications. But since the most crucial aspect of comparative studies was to "find indications of genetic connection," even hypothetical relations were encouraged.[97]

The published work of Haeckel and Gegenbaur represented the only general sources of information concerning evolutionary morphology by 1875. Both authors drew heavily upon the important research of Kowalewsky. Additional information came from the work that, like the studies of Kowalewsky, was undertaken at the Naples Zoological Station by Anton Dohrn (1840-1909), E. Ray Lankester (1847-1929) and F. M. Balfour (1851-1882). By 1875, these sources had so strongly influenced biological work that an evolutionary morphology program with its own unique set of problems and methods could be recognized. One should not, however, assume that the situation was completely unified. There were major differences between the principles for studying morphology from Darwin, Gegenbaur and Haeckel.[98] But for a period of over twenty years following Haeckel's Generelle Morphologie (1866), questions dealing with evolutionary reconstruction dominated evolutionary morphology. By 1875, the tunicate theory had been generally accepted by the morphologists to "bridge the gap" between vertebrates and invertebrates,[99] homologies were determined on the basis of the embryological germ layers and primitive organisms were the subject of the search for connections between protozoans and metazoans.

While most of this work was European in origin, it exerted a strong effect on the character of American morphological studies that were to be undertaken between 1875-1900. It has often been argued that this influence was in the form of encouragement for the construction of genealogical trees[100]; but a closer examination reveals many more sophisticated and penetrating questions. Kowalewsky's work on the tunicate theory of vertebrate ancestry was the inspiration behind impressive American descriptive studies of

Amphioxus, Salpa, Phoronis, Balanoglossus, Sagitta and other organisms. The exact criterion for homology was widely debated. While the Gastrae of Haeckel was generally applied as an embryological criterion for homology, more refinements were pressed after 1875. One major question involved whether the mode of germ layer origin revealed the evolutionary heritage or whether it was the fate of the germ layer that was more important. The coelom theory of development formulated by the Hertwigs and E. Ray Lankester was also debated by American workers. In addition, American biologists conducted sophisticated studies of the life histories of many lower animal forms following Haeckel's encouragement. This information was most often used for genealogies, but much of it was of value for its own anatomical or embryological application.

A much better understanding of the exact character and development of evolutionary morphology following 1857 can be obtained by examining in detail the morphological work of William Keith Brooks. Trained by Louis and Alexander Agassiz at the MCZ and educated during the dominance of the descent theory of Darwin, Brooks began his career as a practicing biologist at Johns Hopkins University in 1876. The important role Brooks and the program at Johns Hopkins had for late nineteenth century was based upon the fact that Johns Hopkins offered the first graduate department in biology in the United States. Together with the MCZ, it served as a main center for American biological education. It was from this department that Brooks conducted his morphological work and offered training in morphology. As a classical "nineteenth century embryologist,"[101] Brooks's scientific investigations generally centered about the study of the development of specific structures and the tracing of the fates of various germ layers. Much of this work was typically morphological, having a descriptive and observational nature. However, in addition to the application Brooks's work had to evolutionary history and genealogical speculation, it also served as important material upon which later experimental studies would draw. Evolutionary morphology, therefore, as practiced by Brooks and others in the United States, was not merely an end in itself nor was it dedicated only to phylogenetic questions. Indeed, the refinements of questions, problems, techniques and methods between 1875-1900 bears witness to the growth in sophistication of the morphological approach in biology and to its importance in the history of the development of American biology.

NOTES

CHAPTER ONE

1. Ernst Haeckel, The Evolution of Man. A Popular Exposition of the Principal Points of Human Ontogeny and Phylogeny. Two Volumes (Akron, Ohio: The Werner Company, 1876). Vol. I, p. 20.

2. At the beginning of his Elements of Comparative Anatomy (London: Macmillan and Company, 1878), Carl Gegenbaur overtly divided the study of morphology into these two subdivisions. While the distinction was a real one among morphologists, it was not restrictive. Morphologists typically worked in both anatomy and embryology, usually depending upon the problem under investigation.

3. Carl Claus, Elementary Textbook of Zoology, translated and edited by Adam Sedgwick (4th ed.; London: Swan Sonnenschein & Co., 1892), p. 52.

4. Louis Agassiz, Contributions to the Natural History of the United States of America (Boston: Little, Brown and Company, 1857), Vol. I, Part 1, "Essay on Classification."

5. Charles Darwin, On the Origin of Species, edited by Ernst Mayr (Facs. 1st ed.; Cambridge, Mass.: Harvard University Press, 1964).

6. Edward Lurie, Louis Agassiz: A Life in Science (Chicago: University of Chicago Press, 1960) provides the best biographical information upon Agassiz.

7. David Starr Jordan, "Agassiz at Penikese." Popular Science Monthly 40 (1892), p. 722.

8. "Louis Agassiz," American Naturalist 33 (1898), p. 153.

9. The article, "Penikese Island" (Harper's Weekly, August 9, 1873, pp. 701-702) includes the announcement for the program of the laboratory. For accounts of Penikese, see the following articles written by students and faculty members of the Anderson School: David Starr Jordan, "Agassiz at Penikese," Popular Science Monthly 40 (1892), pp. 721-729; Alpheus S. Packard, "The Philosophical Views of Agassiz," American Naturalist 32 (1898), pp. 159-164; Burt G. Wilder, "Agassiz at Penikese," American Naturalist 32 (1898), pp. 189-196; Edward S. Morse, "Agassiz and the School at Penikese," Science 58 (1923), pp. 273-275. A later account of the school is recorded by L. C. Cornish, "Agassiz's

School on Penikese - 70 Years After." Scientific Monthly 57 (1943), pp. 315-321.

10. Louis Agassiz, "Essay on Classification," p. 78 and M. P. Winsor, Starfish, Jellyfish and the Order of Life (New Haven and London: Yale University Press, 1976), p. 130.

11. Louis Agassiz, "Essay on Classification," p. 78.

12. "Penikese Island," Harper's Weekly, p. 702.

13. Burt Wilder, "Agassiz at Penikese," p. 191-193 and Ralph W. Dexter, "From Penikese to the Marine Biological Laboratory at Woods Hole—the Role of Agassiz's Students," Essex Institution Historical Collection 110 (1974), pp. 151-161.

14. Louis Agassiz and A. A. Gould, Principles of Zoölogy: Touching the Structure, Development, Distribution and Natural Arrangement of the Races of Animals, Living and Extinct (Boston: Gould and Lincoln, 1849).

15. Editions were subsequently republished from 1851-1861, 1863-1870, 1872, 1873, 1879 and 1880.

16. Louis Agassiz and A. A. Gould, Principles of Zoölogy (1866 edition), p. 5.

17. Ibid., p. 5.

18. Ibid., p. 5.

19. Erik Nordenskiöld, The History of Biology: A Survey (New York: Tudor Publishing Co., 1935), p. 363.

20. The interpretation of Cuvier is from William Coleman, Georges Cuvier, Zoologist: A Study of the History of Evolution Theory (Cambridge, Mass.: Harvard University Press, 1964).

21. Edward Lurie, Louis Agassiz, p. 83.

22. Louis Agassiz and A. A. Gould, Principles of Zoölogy, p. 154.

23. Ibid., p. 29.

24. Ibid., p. 30.

25. The exact definition of homology and analogy underwent a gradual evolution in the late nineteenth century. As indicated above, homology and analogy were originally closely tied to the type concept. After Darwin, this connection was removed. Homologies were considered to be morphological in nature while

analogies were physiological. These relationships could be applied to organisms no matter how distantly related. Haeckel introduced an embryological criterion that based homologies upon common germ layers. This embryological basis became standard toward the end of the nineteenth century. Throughout this period it was also considered that homologies were much more important for systematic considerations than were analogies.

26. The "Essay on Classification" has recently been republished as Louis Agassiz, Essay on Classification, ed. by Edward Lurie (Cambridge, Mass.: The Belknap Press, 1962).

27. Ibid., p. 77.

28. Ibid., p. 78.

29. Ibid., pp. 3-4.

30. Ibid., pp. 79-83.

31. Ibid., p. 84.

32. Ibid., p. 29.

33. Ibid., p. 32.

34. Ibid., pp. 104-110.

35. Ibid., p. 110.

36. Ibid., p. 112.

37. Ibid., p. 113.

38. Ibid., p. 115.

39. Ibid., p. 119.

40. Ibid., p. 182.

41. Ibid., pp. 183-184.

42. Ibid., p. 86.

43. Ibid., p. 87.

44. Ibid., p. 86.

45. M. P. Winsor, Starfish, Jellyfish, pp. 100, 130.

46. All of these men (Hyatt, Morse, Packard, Putnam) were involved in the foundation of the Peabody Academy of Science in Salem, Massachusetts, and in the publication of the American Naturalist (1867). It is interesting to note that all of these men began their work in embryology under Agassiz but switched to paleontology in the mid-1860's. This change was probably facilitated by the fact that all of them worked with organisms that had a rich and, in many respects, almost complete fossil record. It is also notable that the switch in research interests was accompanied by a change from a sympathetic position vis-a-vis Darwin to an overt stand in favor of neo-Lamarckian evolutionary principles.

47. A. S. Packard, "A Century's Progress in American Zoology." American Naturalist 10 (1876), p. 596.

48. Ibid., p. 596.

49. Wesley R. Coe, "A Century of Zoology in America," in A Century of Science in America with Special Reference to the American Journal of Science, 1818-1918, ed. by E. S. Dana and Charles Schuchert (New Haven: Yale University Press, 1918), p. 406.

50. A. S. Packard, "Philosophical Views of Agassiz," p. 159.

51. Ibid., p. 159.

52. Patrick Geddes, "Morphology," Encyclopaedia Britannica, 9th edition, 1883, Vol. 16, p. 840.

53. E. S. Russell, Form and Function, A Contribution to the History of Animal Morphology (London: J. Murray, 1916), p. 246.

54. Patrick Geddes, "Morphology," p. 840.

55. E. S. Russell, Form and Function, p. 247.

56. William Coleman, "Cells, Nucleus and Inheritance: An Historical Study," Proceedings of the American Philosophical Society 109 (1965), p. 126.

57. Charles Darwin, Origin of Species, pp. 412-413.

58. Ibid., p. 420.

59. Ibid., p. 422.

60. Ibid., p. 434.

61. Ibid., p. 434.

62. Ibid., p. 449.

63. Ibid., p. 450.

64. Ibid., p. 338.

65. Charles Darwin, The Variation of Animals and Plants under Domestication, two volumes (London: John Murray, 1868), Vol. II, p. 364.

66. Charles Darwin, The Descent of Man and Selection in Relation to Sea, two volumes (New York: D. Appleton and Company, 1872), Vol. I, p. 24.

67. Thomas H. Huxley, "On the Classification of the Animal Kingdom," American Naturalist 9 (1875), p. 66.

68. Charles Darwin, Origin of Species, p. 427.

69. George G. Simpson, "Anatomy and Morphology: Classification and Evolution, 1859 and 1959," Proceedings of the American Philosophical Society 103 (1959), p. 289.

70. A. S. Packard, "A Century's Progress . . .," p. 597.

71. Wesley R. Coe, "A Century of Zoology . . .," p. 410.

72. Ibid., p. 412.

73. A. S. Packard, "The Philosophical View of Agassiz," p. 163.

74. Ibid., p. 163.

75. David Star Jordan, "Agassiz at Penikese," p. 728.

76. E. S. Russell, Form and Function, p. 247.

77. Ibid., p. 247.

78. Ibid., p. 309.

79. Oscar Hertwig, "The Growth of Biology in the Nineteenth Century," Annual Report of the Smithsonian Institution, 1900 (Washington, D. C.: Smithsonian Institution, 1900), p. 469.

80. E. G. Conklin, "The World's Debt to Darwin," Proceedings of the American Philosophical Society 48 (1909), p. xxxix.

81. Ibid., p. xli.

82. Garland Allen, Life Sciences in the Twentieth Century (New York: John Wiley & Sons, 1975), pp. 2-4.

83. The only other zoological text, other than natural history, was T. H. Huxley and H. Newell Martin, A Course of Elementary Instruction in Practical Biology (London: Macmillan and Company, 1875) which was revised and published also in the United States beginning in 1876.

84. The organisms Kowalewsky examined included the following species: various ascidians (Chordata-urochordate), Amphioxus (Chordata-cephalochordate), Phoroms (Phoronida), Sagitta (Chaetognatha), Echinus and Ophiura (Echinodermata).

85. Roberta Beeson, "Bridging the Gap . . .," p. 111.

86. Ernst Haeckel, The Evolution of Man, Vol. I, p. 196.

87. Roberta Beeson, "Bridging the Gap . . .," pp. 115-116, 128, 131.

88. Charles Darwin, The Descent of Man, p. 160.

89. Ernst Haeckel, The Evolution of Man, Vol. I, p. 5.

90. Ibid., pp. 462-463.

91. Ibid., p. 232.

92. Roberta Beeson, "Bridging the Gap . . .," p. 340.

93. Ibid., p. 192.

94. Carl Gegenbaur, Elements of Comparative Anatomy, translated by F. Jeffrey Bell (London: Macmillan and Co., 1878), p. vii.

95. Ibid., p. 63.

96. Ibid., pp. vii-viii.

97. Ibid., p. 67.

98. Roberta Beeson, "Bridging the Gap . . .," p. 376.

99. Ibid., p. 363.

100. This is the position that has been taken in most historical treatments of the nineteenth century. In particular, Russell, Coleman, Oppenheimer, Nordenskiöld, Allen and others have developed such an appraisal.

101. Garland Allen used this phrase to describe T. H. Huxley, F. M. Balfour, Alexander Kowalewsky, Fritz Müller and W. K. Brooks (Garland Allen, Life Sciences in the Twentieth Century, p. 21). Brooks's inclusion with such an eminent group of investigators provides a degree of his probable importance in the nineteenth century. It should be pointed out, however, that his interests in biology should not be listed as confined to embryology. In a broader sense, Brooks represented the morphological approach in biology; that is, his work was in comparative anatomy and embryology.

Chapter Two: Biographical Sketch of the Personal and Professional Life of William Keith Brooks[1]

William Keith Brooks was born in Cleveland, Ohio on March 25, 1848, the second of four boys.[2] His parents, Oliver Allen (1814-1892) and Ellenora Bradbury Brooks (n.d.), both traced their family origin to English ancestors who settled in Massachusetts in the 1630's.[3] The senior Brooks moved to Cleveland from Burlington, Vermont in 1835 and began an import shop called "Huntington and Brooks" in 1837. After the birth of his sons he changed the name of the business to "O. A. Brooks and Sons, Importers and Wholesale Dealers in Earthenware, etc." It was obvious that he desired his sons to follow him into the business.

William Keith's childhood was a fairly normal one. Although a congenital heart condition kept him from leading an extremely active life as is typical of many small boys, Brooks developed an early interest in natural history. According to his older brother Oliver (1845- ?), there were several influences that served to nurture this early interest in Brooks.[4] The first was that the Brooks home was located in an area adjacent to the surrounding countryside. The boys spent much of their time in the outdoors. William used these experiences to collect all kinds of natural history artifacts, from rocks to feathers to plants. Brooks's grandfather, the Reverend Phineas Kingsley (1788-1863), had also moved to the Cleveland area and lived on a small farm. It was here that Brooks spent many Saturdays and holidays, either exploring the countryside or reading Thomson's History of Vermont and Smellie's Philosophy of Natural History from his grandfather's small library. Another relative, his uncle I. F. Warner (n.d.) who lived across the street from the Brooks, had noticed William's interest in natural history. For Christmas in 1862, he gave Brooks a copy of Wood's Illustrated Natural History.[5] Brooks consulted the book extensively, often sketching in the margins or offering critiques for Wood's treatment of natural history (the "Ruby-throated Humming-bird" illustration was annotated by Brooks as having "Bill to [sic] Short").[6] Another neighbor was J. S. Newberry (1822-1892), who later was a geologist at the School of Mines at Columbia College. Several of Newberry's sons were companions and playmates with William. He often had the opportunity of accompanying the Newberry family on geological excursions and field trips. Brooks also began his own collection of fossils and geological specimens, the collection being patterned after Newberry's own large exhibit which he kept in his home. Brooks's geologizing continued into his adolescent years when he formed a friendship with Colonel Charles Whittlesey (1808-1886), a geologist and mineralogist. Together they investigated the area in the valley of the Cuyahoga River.[7] At the same time, a local physician and amateur naturalist, Dr. Kirtland (1793-1877),[8] taught Brooks how to preserve various faunal materials. The natural history collection soon took over the upper story of the family barn. The collection was impressive with shells, fossils, minerals, other geological specimens, stuffed birds and mammals, and jars of preserved specimens. All were carefully arranged, classified and labeled. The last major influence came from Charles F. Brush (n.d.), who presented Brooks with a microscope, a rare tool for such a young investigator. Aided by the assistance of the retired physician, Dr. A. Maynard (n.d.), Brooks learned to operate the microscope. Dr. Maynard also taught Brooks some elementary histological techniques, he gave him instruction in making lenses and he allowed him free access to his private and extensive library.

Brooks's formal education was in the public schools of Cleveland. He was a quiet, but attentive student. Due to these characteristics, he became nicknamed "Mummy" at an early age. In high school, his interest was in mathematics, Greek and the natural sciences. One of his achievements during these years was to organize a society, "Magnus Pax," dedicated to reading selected works and discussing them.

Brooks left high school at the end of the eleventh year and enrolled at Hobart College in 1866. Brooks stayed at Hobart for only two years, but they were beneficial years. First, he became the first freshman in the history of the college to win the "White Essay Prize,"[9] the annual award for the best essay written by a student during the academic year. Second, it was at Hobart that he first read works of Charles Darwin. These books were to have a profound impact on his professional career. Finally, Hobart provided him with his first exposure to philosophy, an interest that continued throughout his life. In particular Brooks became seriously interested in the work of George Berkeley (1685-1753). The influence of Berkeley was so profound that Brooks wrote in the dedication of his synthetic work on biology, The Foundation of Zoology:

> To Hobart College, where I learned to study and, I hope, to profit by but not to blindly follow, the writings of that great thinker on the principles of science, George Berkeley.[10]

In 1868, Brooks moved to Williams College where he continued his interest in natural history, Greek and mathematics. For botany and zoology, he studied under Sanborn Tenney (1827-1877).[11] He also attended the frequent lectures at the Lyceum of Natural History at Williams, an organization that encouraged active participation in field trips and excursions.[12] His mathematical work at Williams was excellent and "he was generally acknowledged to have been the most brilliant student in mathematics Williams had ever seen."[13] Brooks graduated Phi Beta Kappa in 1870.

When Brooks graduated he had decided on a career in teaching but he could not select between biology, Greek and mathematics. The situation was compounded by a less than favorable attitude from his parents. Brooks's father was of a practical persuasion and felt education was only valuable for its application to business. As a result, Brooks was convinced to join the "O. A. Brooks & Sons" venture. However, Brooks was not content with the situation. Noting his son's displeasure, the elder Brooks sought the advise of the family physician, Dr. Maynard.

> The Doctor [Dr. Maynard] told him [a friend of Dr. Maynard's] that my father [O. A. Brooks] at one time came to him in a good deal of perplexity, to ask his advise about Will, who had then been taken into his store, but who showed no interest in business and no inclination for it, but, on the contrary, seemed to have his mind occupied with other matters which had no relation to business, and of which my father could not see use. The Doctor had seen a good deal of Will, and Will had talked with him pretty freely about the subjects and studies which attracted him, and he told my father he thought it was better to let Will follow his evident inclination for a life of study and research, believing he would never adapt himself to a business life and would only be made unhappy by being confined to an uncongenial occupation, but that he was in no danger of becoming a mere loafer, and, on the contrary, had ability which would become evident if he were allowed to follow his inclinations, and that if so allowed the boy would show he had good stuff in him and a mind above the ordinary, and would probably succeed.[14]

Brooks's father was convinced, and Brooks was allowed to leave the business after one year's service.

At some point during his short tenure in business, Brooks evidently decided that his preference for employment and education resided in the field of biology. In the fall of 1871, he accepted a teaching job in natural history at DeVeaux College in Niagara, New York. The college was a boarding school providing preparatory education for boys planning on higher education. From the notes of former students, Brooks was an outstanding teacher at DeVeaux. His classes were popular, due in part to the many student expeditions Brooks led to examine the geology, flora and fauna along the Niagara River.[15]

The position at DeVeaux placed Brooks in a financial position that would allow him to continue his education. During the winter of 1872-1873, he received a circular announcing a "Programme of a Course of Instruction in Natural History, to be delivered by the Seaside, in Nantucket, during the Summer Months, chiefly designed for Teachers who propose to introduce the Study into their Schools and for Students preparing to become Teachers."[16] The brochure came from Louis Agassiz, the well-known professor of zoology and geology at Harvard. Agassiz proposed the course as a scientific "camp-meeting" where workers in natural history and teachers of biology could mingle.[17] Agassiz was convinced that most instruction available in natural history was taken directly from what textbooks were available and, consequently, was presented in a very mechanical manner. By offering a summer school in which direct observation of natural phenomena was stressed, he hoped to change this trend. The prospect of attending the summer session appealed to Brooks so he applied to receive additional information.

As late as March of 1873, Agassiz was still not sure where the session was going to be held or what the financial arrangements would be.[18] While the original site suggested was Nantucket, before it was definitely chosen John Anderson, the wealthy New York tobacco merchant, presented Agassiz with the island of Penikese, a large yacht to aid in collection and an endowment of $50,000.[19] Thus, the Anderson School of Natural History was established on the small rocky island located in Buzzard's Bay, halfway between New Bedford, Massachusetts and Martha's Vineyard.

Brooks was among the "many hundreds" who applied for admission and also was one of the fifty who were accepted. Of those accepted, forty-four (twenty-eight men and sixteen women) attended the school when it opened in June of 1873.[20] For instruction, Agassiz had invited many working scientists to come to Penikese, both to work and to provide practical instruction and guidance. Formal courses were not included, although several lectures by various professionals were presented. Among the twenty natural historians who accepted Agassiz's invitation were the following: Burt G. Wilder of Cornell, Alpheus S. Packard from the Peabody Academy of Science, Count L. F. Pourtales (1824-1880) of the Coast Survey, Waterhouse Howkins (n.d.) from England, Paulus Roetter (n.d.), artist from the MCZ, Professor H. Mitchell (1830-1902) of the Coast Survey, Josephy S. Lovering (1813-1892) in mathematics and natural philosophy from Harvard, F. W. Putnam from the Peabody, N. S. Shaler (biology) from Havard, Arnold Guyot (1807-1884) from Princeton and Professor C. E. Brown-Sequard (1817-1894).[21]

The typical approach of Agassiz to education was followed at Penikese. Independent investigation by the students was paramount. Furnished with all the necessary scientific instruments and implements, they were directed away from authoritarian courses. Instead, the instructors constantly encouraged the participants to study, observe and discover on their own. In Agassiz's opening address, this methodology was made explicit.

> There is one thing of which I am certain, that we do not begin our task by reading, by using any report of others concerning the objects to which we will turn our attention. We are, I suppose, all intelligent enough to open our eyes and look upon nature for ourselves, and we will try to make nature as it surrounds us its own textbook. If I can I will try to make you investigators, to teach you to find out what you want to know for yourselves, that you may be able to do the same thing in other places where you may have no guide.[22]

As the motto that was conspicuously placed in the laboratory at Penikese stated, Agassiz's goal was to "Study Nature, Not Books."[23] Both Agassiz's message and his methodology became firmly impressed upon Brooks. He was later to use a remarkably similar approach in his own instruction.

The summer on Penikese must have been a pleasant experience for all those involved. David Starr Jordan recorded his own impressions of the time spent with Agassiz.

> And the summer went on with its succession of joyous mornings, beautiful days, and calm nights, with every charm of sea and sky, the master with us all day long, ever ready to speak words of help and encouragement, ever ready to give us from his own stock of learning. The boundless enthusiasm which surrounded him like an atmosphere, and which sometimes gave the appearance of great achievement to the commonest things, was never lacking.[24]

Brooks, too, was sufficiently impressed with Agassiz, with his exposure to the marine environment and with others from the MCZ that he requested to enter the Lawrence Scientific School in the Fall of 1873. Brooks was accepted to study under Agassiz, but unfortunately his exposure to Agassiz was brief for Agassiz died in December of 1873. Nevertheless, Brooks continued at Harvard and pursued his new found interest in marine organisms.

The death of Louis Agassiz created a distinctive gap for instruction in zoology at Harvard. Alexander Agassiz assumed control over the MCZ but did little in the way of offering instruction. John McCrady, who had taken charge of the instruction in zoology shortly before Agassiz's death, continued from 1873-1877 to conduct the work of the biological sciences. In spite of the fact that he had previously served as Professor of Mathematics in the College of Charleston (South Carolina), at Harvard he was in charge of the supervision of research students (graduate students), he gave both the elementary and advanced courses in general zoology, and he supervised the laboratory instruction. He was partially aided by William James (1842-1910) at the MCZ, who taught comparative anatomy and physiology of vertebrates.[25.]

Despite the problems that the biological protion of the Lawrence School was experiencing in the 1870's, the first four doctoral degrees in zoology were awarded during this time.[26] Brooks was able to overcome the deficiencies of the department in his graduate program by utilizing several different sources. Having become acquainted with Alexander Agassiz at Penikese in 1873, Brooks had access to the equipment, laboratories and resources of the MCZ. In addition, Agassiz had encouraged Brooks to continue his interest in marine invertebrates, pointing out to him the need to investigate tunicates and their relationship to the phylum Chordata. Brooks accepted this challenge, attended the Anderson School of Natural History in the summer of 1874 (its second and last year of existence) and obtained study specimens of the tunicate genera Salpa. He continued this research at the MCZ and at Agassiz's private marine laboratory in Newport, Rhode Island in the early summer of 1875. Brooks also made maximum use of Professor McCrady. Although he was professionally trained as a mathematician, McCrady had wide-ranging interests. In addition to a penchant for philosophical ramblings, he had conducted an extensive survey of the various hydromedusae in Charleston, South Carolina. The work proved to be extremely interesting to Brooks and served as the primary basis upon which a later study of mid-Atlantic hydromedusae would be based. Finally, Brooks sought out various authorities to assist him with the subject of an investigation he had started at DeVeaux on freshwater mussels. In this regard, work with Alpheus S. Packard and E. S. Morse at the Peabody Museum and instruction from Alpheus Hyatt at the Boston Society of Natural History proved to be most valuable.

The combined result of the guidance available to Brooks was several impressive investigations that served to place Brooks in the position of an established scientist even before he had completed his doctorate. In 1874, he presented a paper on his early research upon a freshwater mussel, "On an organ of special sense in the lamellibranchiate genus Yoldia,"[27] to the Hartford meeting of the American Association for the Advancement of Science (AAAS). The completed study of the group was presented the following year at the AAAS meetings in Detroit.[28] The paper and publication that followed were regarded by several investigators as the most important work on the embryology of the freshwater molluscs.[29] A similar reception was given to his work, "Embryology of Salpa,"[30] which was the result of his investigations with Alexander Agassiz on the pelagic tunicates.[31]

While he was training to be a zoologist at Harvard, Brooks lived with several other students in the old wooden building known as Zoological Hall, near the present site of the Peabody Museum.[32] The most characteristic features that others stressed concerning his personality included his contemplative nature, his unkempt appearance and his constant companion, a large Saint Bernard named "Tige." He led a very studious and solitary life, either reading alone in his room or working long hours in the laboratory with his sketching materials and microscope. Edward A. Birge (1851-1950) noted that much of Brooks's reading included the major works on the central problems in biology. In particular, Brooks spent much time reading Charles Darwin. Brige stated that one day,

> he brought me a new copy of Darwin's Origin of Species, and when I asked him what this meant, he told me that he had borrowed mine one day when I was out, and, having kept it a good while, had written so many notes in it that he preferred to buy me a new copy rather than give me the old one back.[33]

Like many of his contemporaries, Darwin's work became very important for Brooks. As will be shown later, his interest in and adherence to the major points in the Origin of Species was a marked characteristic of his scientific work.

After graduating from Harvard in 1875, Brooks returned to Cleveland for two months to organize a summer program for teachers of natural history. With Albert H. Tuttle (1844-1927) and Theodore B. Comstock (1849- ?), both former childhood companions of Brooks, the "Kirtland Natural History Society" was founded. While the effort started with a small enrollment, added financial resources provided the necessary means to attract over twenty-five teachers. The model for the program was, of course, the Anderson School of

Natural History. In typical fashion, lecture and textual instruction were downplayed in favor of laboratory meetings and field excursions.[34] The remainder of the summer, August and September, Brooks spent with the salp work at Agassiz's Newport laboratory. To support himself financially at Newport, Brooks also offered instruction in natural history to local high school students.

Brooks's initial professional position following his completion of the doctorate was in the museum of the Boston Society of Natural History. Alpheus Hyatt placed him in charge of the entire mollusc collection, a job Brooks attacked with his characteristic fervor and dedication. Despite his adeptness at museum work, Brooks realized that it was not to be his chosen profession. Apparently Alexander Agassiz was aware that Brooks desired another situation. When the Johns Hopkins University announced the opening of the school in 1876, the availability of twenty fellowships for advanced study and the formation of America's first graduate Biology Department, Agassiz wrote to Daniel Coit Gilman (1831-1908),[35] the president of Johns Hopkins, an unsolicited letter recommending Brooks for one of the fellowships. While the letter contained some reservations about Brooks personal habits, it was extremely positive concerning his professional prospects.

> I have here among the students who have just taken (last fall) their degree of Ph.D. a young man named Brooks who studied with McCrady two years, was with me at Newport last summer and who has done some excellent original work--what he did last summer I should not be ashamed of myself. I could as far as his ability and integrity is concerned recommend him most earnestly

> for a Scholarship in Natural History. He has had a little practice in teaching, he is not a very cultivated man but is good at heart and extremely anxious to devote himself to Natural History, while his friends wish him to go into business and he has only this year left to look about. He has in him if I am not mistaken the making of an excellent original worker, but he is a specialist and has much to learn in a general way. I have said nothing to him about applying.[36]

Within a month, Brooks was informed of the position at Johns Hopkins, personally wrote to President Gilman acknowledging Agassiz's recommendation and requested more information concerning the "scolarship [sic] in Natural History."[37] Upon receiving the material from Gilman, Brooks tentatively decided to pursue the fellowship in earnest. He sent Gilman his three published papers (two on the freshwater mussel and the other on Salpa) along with two unpublished manuscripts. The latter also included, for references, the names of the publication committee at Harvard, Professors John McCrady, Alexander Agassiz, Alpheus Hyatt, A. S. Packard and E. S. Morse.[38]

All of those whom Brooks recommended to provide the fellowship committee at Johns Hopkins with references, responded extremely favorably. Extracts of these letters illustrate the high regard several of the leading men in American biology had for the potential of Brooks. John McCrady wrote,

> Mr. Brooks has been my student in Zoology for about two years--he has an unusually high order of ability for original research in his science, and has already done work such as has quite transformed certain subject upon which some of the best observers in the work had previously been (less successfully) engaged. I think no young naturalist in America has at present equal claims for such a position as he seeks; and I think you will find him a decided acquisition to the staff of the University.[39]

Alpheus Hyatt had a similar opinion concerning Brooks. In a letter he sent to Brooks relating to the recommendation to Johns Hopkins, he stated that he had

> read this [Ph.D. thesis] carefully, and have no hesitation in recommending it highly for the thoroughness and accuracy of the details, so far as I could judge of them without making special investigations for that purpose. It must be remembered, also, that it represents a large amount of patient labor in the most difficult department, microscopical embryology.[40]

Hyatt also commented that Brooks had provided him with "complete satisfaction" as his assistant in the museum of the Boston Society and that Brooks had "materially improved" the mollusc collection with his preparations of "great value."[41] E. S. Morse wrote that the thesis of Brooks was the "most original contribution of its kind on the subject."[42] In a more detailed letter, A. S. Packard made a similar point.

> . . . it [Brooks's thesis] struck me as an original and important paper upon a difficult theme. The work seemed to have been thoroughly done and the subject treated from the standpoint of the more advanced ideas in Zoology. It extends and supplements the papers of distinguished German naturalists and is by far the most exhaustive treatise on the subject I know of.
>
> Though I have not been requested to do allow me to allude to a partly published memoir of Dr. Brooks on Salpa, its organization and development, places him as an independent and original investigator, in the front rank of our younger scientists.[43]

With such support, it is not surprising that Brooks was selected from several hundred applicants as one of the twenty fellows to attend Johns Hopkins. Brooks made a provisional acceptance of the offer in June, 1876.[44]

It was Daniel Coil Gilman's conscious desire to pattern the graduate program at Johns Hopkins University after the German university model. The emphasis was to be upon the "prosecution of special advanced studies."[45] To aid him in his planning, Gilman sought the advise of T. H. Huxley. The enlistment of Huxley's service was a commendable decision. Except for Harvard, American colleges hardly covered the subject of biology so there were no models in the United States for Gilman to follow. And, it was recognized among the international zoological community that the best biology work was being done in Europe. English physiology was very sophisticated and German studies upon cell division and development were universally recognized.[46] All of these facets of biological work and education were familiar to Huxley. His advise to Gilman was to hire a young physiologist, H. Newell Martin (1848-1896), who had worked with Sir Michael Foster (1836-1907) and in Huxley's own laboratory.[47] Huxley noted that there was a "favorable prospect" for Gilman to obtain the "cooperation of Dr. Martin."[48] In other words, H. Newell Martin was available for the position.

In Gilman's letter to Dr. Martin, his bias to establish a Biology Department upon the European model was obvious.

> I suppose the work to be done among us will be to organize a laboratory and school of biology on a plane similar to that of Prof. Huxley at So. Kensington with the belief that the instructions will be followed by two classes of young men, first chiefly by those who propose subsequently to study medicine and second those who expect to become naturalists.[49]

Martin was sympathetic with the program but had two strong reservations that caused him to decline the position.[50] The first was a financial matter that was quickly resolved by Gilman and appeared to have caused Martin to change his mind and accept the position.[51] The second matter was that Martin felt the Biology Department should have someone trained in morphology as a faculty member to balance his own physiological background. Alexander Agassiz had made a similar suggestion to Gilman. Again, heeding the advise of those more knowledgeable in a specific field than himself, Gilman decided to offer William Keith Brooks the position of Assistant in the Biology Department.

Brooks's own decision to attend Johns Hopkins was made with some reservation. For several years he had been living on a limited income as a student in Cambridge and as an assistant in the Boston museum. When Hyatt heard of Brooks's acceptance at Johns Hopkins, he made an attractive counter-offer in a futile effort to keep Brooks at the Boston Society. Brooks also was presented an offer of a professorship in natural history at the University of Cincinnati. Therefore, when Brooks received a letter from P. R. Uhler, a naturalist hired to direct the museum work at Johns Hopkins, asking Brooks to allow him to submit Brooks's name as Martin's assistant, he made a guarded reply.

> If I felt at liberty to decide according to my own interest I should unhesitatingly accept the offer which you propose so kindly; but as the matter stands I feel obliged to make my choice rest, in part at least, upon the question of pay, and must therefore ask, before allowing you to propose my name as Dr. Martin's assistant, what will be the salary of this position.[52]

The financial arrangements were decided upon later in the summer and Brooks accepted the position.

Despite the fact that Martin was originally the only member of the Biology Department, from the outset the department did not intend to promote exclusively physiological studies, Martin's specialty. Indeed, Martin made a concerted effort to emphasize that the department was to be based upon the two great ideas in biology, the doctrine of evolution and the conservation of energy.[53] To address these themes, a mixture of morphological and physiological courses would be offered. This direction would be followed, moreover, despite the fact that the majority of the students were of a medical persuasion and, therefore, more inclined toward physiological interests. Martin noted that the morphological aspect would be developed as demand from students warranted.

> On the zoological and morphological side no arrangements have as yet been made for a lecture and laboratory course this year, nor so far as I know has any such demand as would render it advisable shown itself. Should it do so, however, we may, perhaps, make arrangements for elementary instruction in those subjects under the more immediate supervision of Dr. Brooks, our associate in biology, upon whose shoulders I must throw most of the burden of that side of the work. We shall, at any rate, collect material and make other preparations for such a course next year. After Christmas Dr. Brooks will give a course of lectures on "Morphological Theories."[54]

When the department opened in the fall of 1876, "General Elementary Biology" was offered from both Martin and Books, and "Animal Physiology and Histology" was offered by Martin. In addition, advanced courses and research were available to conduct physiological work.

> The laboratory will be very completely fitted up, and so far at least as regards physiology will present facilities for work unequalled, it is believed, in this country, and excelled by but few laboratories abroad. . . . The collection of instruments for experimental physiology will be very complete,

> including the best used in every department of physiological work, and will be added from time to time, as special instruments may be required.[55]

During the opening fall, Brooks had little direct morphological work to do. His duties were restricted to the morphological instruction in the "General Elementary Biology" course. In a letter to Alexander Agassiz thanking him for his role in obtaining the position at Johns Hopkins for Brooks, he mentioned that the lack of instructional duties was in large part due to the number of young physicians and medical students in the department. However, this situation began to change in 1877 when Brooks was in charge of "Comparative Anatomy and Zoology," "Animal Embryology," and a series of sixteen public lectures, "The Theories of Biology."[56] Within a year, Brooks had obtained a following of students and had developed a research program that was on par with the physiological program of Martin.[57] This is attested to by the report filed by Professor Ira Remsen (1846-1927) on the progress in the laboratories, submitted to the president of the University in 1878. As of February 22, 1878, advanced research in physiology was being conducted on the glandular structure of the stomach, the changes in the spinal cord following the severing of selected nerve roots, the life history of pathogenic fungi and the nervous factors in the respiratory mechanism of the frog. At this same time, research activities in morphology included work on the development of _Salmonidae_ and other bony fishes, a study of the embryology and adult structure of _Amblystoma_,[58] and research on the development of Mollusca and its bearing upon the phylogeny of the group and the Gastrae theory of Haeckel.[59] The desired balance in the research activities of the department between physiology and morphology, therefore, appeared to have been achieved by 1878, only two years after the program began.

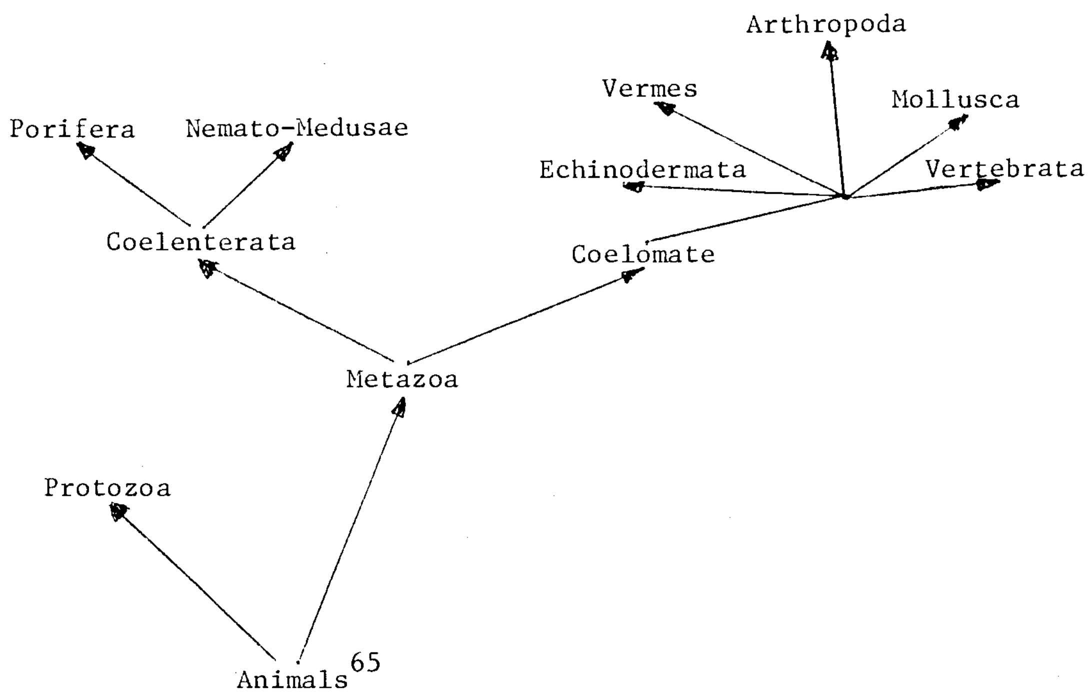
Not only did the biological work of the department illustrate an equal split between morphological studies and physiological studies, but Brooks's own position in the department was changed to reflect the importance of his contribution to the Biology Department. In 1878, the trustees of Johns Hopkins reappointed Brooks to the department with the title of "Assistant Professor of Comparative Anatomy and Zoology."[60] The new status legitimately recognized Brooks's important role in the department. No longer was he referred to as "our associate in Biology" or as "Martin's assistant."

While much of the reason for the initial desire to develop a program in biology was in anticipation of the establishment of a medical school and hospital,[61] the desire of Martin to provide a balanced program in biology, and the work of Brooks to develop a sound morphological background in the department, created the strongest biology program available at the time in America. It is interesting to note that the strength of the department was apart from any possible application to the study of medicine. By 1880, Johns Hopkins offered a well-balanced program. Introductory courses were available in both physiology and zoology. From here, the students were advanced quickly to more sophisticated courses. Brooks offered instruction in morphology, embryology and advanced research. Martin presented an analogous program in physiology.

Not only did the Johns Hopkins department represent the strongest biology program in America at this time, it was also the sole academic institution that offered any advanced laboratory work. Harvard was the only other institution with an established biology program. However, in the early 1880's the department there was still attempting to develop a complete undergraduate and graduate program following the cessation of most advanced training after Agsssiz's death.[62] As late as 1881, in fact, formal laboratory courses were not even available at Harvard. Therefore, in a very real sense, any serious graduate student in biology in America was presented with Johns Hopkins or Europe as the only means to obtain adequate advanced work. This fact illustrates the importance of Johns Hopkins for the development of the American biological community.

The importance of Johns Hopkins presented Brooks with an unparalleled position to develop a strong morphology program. Initially, he offered courses in animal morphology (elementary and advanced), embryology and laboratory instruction.[63] In the early years, osteology, human and comparative, was alternated with the embryology course as a service to the medically-oriented students. However, as the department grew, both in terms of students and faculty, Brooks began to restrict his classes to general zoology for advanced students, elementary zoology and marine zoology. With few exceptions, by 1890 Brooks taught no other courses than the zoology courses.

The general zoology class represented a classical approach to zoology.[64] In the first lecture the students were exposed to a phylogenetic treatment of the entire animal kingdom. Brooks divided all living organisms into Protozoa and Metazoa. Beginning with the protozoans, he minimized their importance by boldly saying they were "less important for us than Metazoa." Then, applying Haeckel's Gastrae theory of ancestral inheritance, Brooks stated that all the metazoans were at one time a single cell and, as a result, in development passed through a stage in which all the cells were alike. With this serving as a foundation, Brooks presented the phylogenetic tree of the animal kingdom as follows:



The remainder of the course was spent in systematically covering all the major taxonomic units of the animal kingdom. Included were detailed discussions of comparative anatomy, embryology and, where appropriate, paleontology. The complete lecture course was presented with the typical clarity of Brooks's style and was often supplemented with vivid illustrations.

> I think my earliest definite recollection of Professor Brooks is of seeing him walk into the lecture room in an undergraduate class wearing a long rubber overcoat which he proceeded at once to use on himself for the purpose of illustrating the morphological relations of the squid's mantle, while holding out the upturned collar to demonstrate the position of the siphon.[66]

In connection with the zoology course for advanced students, Brooks offered an accompanying laboratory course. It was here that graduate students were exposed to the modern techniques and methods to investigate zoological problems. Since many of the phenomena that were dealt with in Brooks's laboratory involved questions of morphological relations and, therefore, an investigation of early developmental stages of organisms, microscopical preparation was stressed. For the beginners, learning microscopes were available. The more advanced students had access to the latest Zeiss microscopes.[67] They were also instructed in the use of various staining strategies, sectioning techniques and slide preparation methods. Many of these practices were recently developed in Germany in the 1870's and 1880's, so the laboratory actually served as a receiving point for these new developments.

Brooks supervised the laboratory in the same unstructured, loose and informal style he had been exposed to under Agassiz. The emphasis was upon the student learning to rely on his personal powers of observation.

> When I began my graduate work in zoology, I was, like every one else at the start, cast adrift, to sink or swim; and for all one knew at the time, Brooks seemed absolutely indifferent as to the outcome. He had given me a bottle containing a few shriveled and collapsed specimens of Doliolum [sic], with instructions to work on the proliferous stolon. I remember with mortification how I floundered helplessly through the first few months in what appeared to me a hopeless struggle to reach solid ground, until one day I happened to find out something new about the stolon. It was a very trivial point, but in the exuberance of my first discovery I showed it to Professor Brooks, and from that moment his attitude toward me changed as if by magic.[68]

Brooks used the same method even for teaching histological technique.

> At one time he had some of his students repeating ancient history in trying to imbed tissues in soap, and to more than one who asked him advise about staining microscopical preparations he recommended Beale's Carmine; the results were always unsatisfactory, but in the meantime the student had learned something about the historical development of staining methods, and, best of all, had also learned to rely upon himself rather than upon Doctor Brooks. One such student, after laboring for some weeks with Beale's Carmine, saw Doctor Brooks and told him that he could not get satisfactory results. After waiting in vain for some response, he ventured to ask whether Doctor Brooks had ever used the method. Yes, he had. "What did you think of it?" "Twasn't worth a damn."[69]

In spite of the lack of direct instruction to his students, they did learn the required tools necessary to conduct investigations into morphological problems. Brooks accomplished this by assigning students to specific research projects in which the student was expected to examine previous work of a similar nature and apply the work to their own projects.

> Most of the advanced work was carried on individually, and not in class; each worker taking up some special topic for study under the immediate direction of some one of the instructors. In addition to the original researches already enumerated,

> certain graduate students have in this manner carried on advanced study in various directions.
>
> Students engaged in this kind of study (which forms a stepping-stone between classwork and original research), are usually given some important original article, and shown how to repeat and verify for themselves (and criticize) the experiments and results described in it. By studying and repeating the original work of others they learn the methods of biological investigation, and are thus trained to plan and carry out researches themselves. In connection with this work, students are also taught how to hunt up and utilize the bibliography of a subject.[70]

In this manner, Brooks expected graduate students to be mature enough that they could learn most efficiently on their own. Such an expectation, when realized by the student, often is much more effective than more overt instruction. In addition, the atmosphere of graduate students working together, older students helping the newer students and the comaraderie that results from such an environment, was probably conducive to effective learning. Another possible explanation for the efficiency of Brooks's instructional methodology is that the students learned by example. Despite the fact that the advanced laboratory was conducted to harmonize with the advanced morphology course, Brooks saw no need of personally becoming involved in the laboratory exercises. Instead, while the students were working, Brooks continued to prosecute his own research activities. It is reasonable to assume that his activities were observed by all in attendance.

The research that Brooks conducted was another factor that served to promote himself and the Biology Department at Johns Hopkins into a prominent position in American science. From the time of his appointment at Johns Hopkins until 1893, the period corresponding to his most active research work, Brooks published no less than ninety-five papers or monographs in various journals. Many of these articles were the result of his personal investigations upon the major problems confronting late nineteenth-century biology.[71] The publications can be generally grouped into the following categories: studies on hydromedusae, dating from his association with John McCrady; investigations on the developmental stages of molluscs, especially in relation to the Chesapeake Bay oyster; work on the nauplius stage of various crustacea, including the specimens from the Challenger expedition; microscopical examinations of selected ascidians, mainly undertaken to determine the relation of this group to the ancestral vertebrates; studies of various groups to investigate the origin of pelagic life; and hypothetical treatments of natural selection, in particular the refinement of Darwin's pangenesis hypothesis.[72] Even after 1893, Brooks remained prolific, with at least fifty-seven publications until the end of his career in 1908. These publications, generally speaking, represent a much more theoretical and speculative phase of Brooks's professional career. They resemble the other papers, nevertheless, in dealing mainly with various questions relating to the descent of species from a common ancestry.

Early in his career, Brooks recognized the problem that faced American investigators in zoology throughout the nineteenth century; there were too few scientific journals to facilitate publication and exchange of scientific information. To address this problem and to create an organ for the publication of research conducted at Johns Hopkins, Brooks founded the short-lived journal, Scientific Results of the Sessions of the Chesapeake Zoological Laboratory. Since this publication included only the results of Brooks's area in the department, it was suggested by President Gilman that a more inclusive journal should be issued from the entire department. With H. Newell Martin and Brooks serving as editors, the Studies from the Biological Laboratory of Johns Hopkins University was established to fill this need. Studies was published from 1879-1893 in five volumes before it was discontinued.[73] In 1887, Brooks secured the permission of the administration to publish a second journal, Memoirs from the Biological Laboratory of the Johns Hopkins University. This publication, with Brooks as editor, was intended to print studies of a more extensive nature than those usually printed in Studies. The Memoirs was also issued in five volumes, the last volume printed in 1903. In addition, Brooks served on the editorial board of the Journal of Experimental Zoology, which began publication in 1904,[74] and the editorial committee of Science, beginning his service in 1895.

Brooks's own publications were not restricted to the journals published by Johns Hopkins. In fact, his strong support for the formation of Studies and Memoirs stemmed from his desire to have a means through which his students could publish their scientific work they completed while still students. Many of Brooks's articles appeared in other publications such as Proceedings of the Boston Society of Natural History, Proceedings of the American Association for the Advancement of Science, Bulletin of the Museum of Comparative Zoology, American Naturalist, Popular Science Monthly (popular articles), American Journal of Science, Memoirs of the Boston Society of Natural History, Proceedings of the Academy of Natural Science, Memoirs of the National Academy of Science, Natural Science, Science, Journal of Morphology, Proceedings of the American Philosophical Society and Publications of the Carnegie Institute of Washington.

That Brooks published in such a wide variety of journals was due to his desire to expose the program at Johns Hopkins to as large an audience as possible.[75] For this same reason, he submitted several papers to the Monthly Microscopical Journal (London), Annals and Magazine of Natural History (London), Zoologisches Anzeiger (Leipzig), Philosophical Transactions of the Royal Society (London), Proceedings of the Royal Society (London), Archives de zoologie, experimental et général (Paris) and Nature (London). Brooks even encouraged his own students to publish outside of the university. This was especially true if Brooks considered the work to be particularly valuable. A clear example is offered by Brooks's letter to President Gilman regarding E. B. Wilson's work on Renilla.

> If he succeeds in finishing his paper this year it will be a monograph which will be highly credible not only to us but to American science and if money can be found to publish it in good shape it will make as valuable and handsome a paper as those from Dohrn's laboratory.[76]

The reference to "Dohrn's laboratory" was to the Naples Zoological Station, the leading institution for developmental studies in the late nineteenth century. To be favorably compared with it would demonstrate the recognition of the work at Johns Hopkins by the international zoological community.

In addition to his attempt to exhibit the work of the Biology Department at Johns Hopkins to the biological community through national and international journals, Brooks was instrumental in insuring that the graduates of Johns Hopkins were well exposed to the current literature. While the journals and monographs available in the United States were admittedly few, this situation was not true in Europe. The problem was that these sources were usually not available in an accessible form in America, either from circulation restrictions or from language difficulties. To remedy this situation, Brooks and Martin instituted a Journal Club that was "composed of the instructors and advanced students, meets weekly for the reading and discussion of recent biological publications."[77] The Journal Club was not formally instituted until the academic year of 1882-1883, but as early as 1880 there was some kind of "Biological Society" for the explicit purpose of reading the newest literature.[78]

The subjects covered by the Journal Club were variable, depending in large part upon the content of the current journals. For example, Winterton Conway Curtis (1875-1975), a graduate student and Ph.D. from Johns Hopkins in 1901, recorded several of the topics covered by the Club during the academic years 1893-1895.[79] An English abstract of the untranslated paper by Otto Maas (1867-19 ?), "Bau und Entwicklung der Cuninenknospen,"[80] dealing with aspects of hydromedusae development, was presented and discussed. Brooks talked about a paper by A. Oka (1868-1944), on budding of Botrylliden,[81] an ascidian, and its relationship to his own work on budding in Salpa. Another paper by A. Jaworowski (1849-1924) on the origin of the arachnid lung[82] was debated since it did not agree with the work of a former Johns Hopkins graduate, Adam T. Bruce (1860-1887). F. H. Herrick (1858-1940) presented a discussion of the work he had completed with Brooks on Macroura. Papers of evolutionary importance were also read. William Bateson's (1861-1926) work on "Variations in males of certain insects expecially in those insects which present much sexual difference,"[83] was the subject of the Club in November, 1892. Brooks also used the reading group as a sounding board for many of his ideas. In December of 1894, he talked at great lengths about the "Fundamental conceptions of life."[84] This was closely followed by another weekly meeting when the subject was "Variation." The next year, the club discussed a number of T. H. Huxley's essays. This brief examination illustrates the breadth of discussion topics entertained by the Journal Club.

In addition to the Journal Club, a more specialized reading group was organized for the year of 1887-1888 for students pursuing morphological studies.[85] The group, known initially as the Morphological Reading Club but later as the Morphological Seminary, was directed solely by Brooks and often met at his home. During the first year, it met weekly to read and discuss Louis Agassiz's

"Essay on classification."[86] By 1892 the Seminary became an integral part of the graduate student's education, stressing the reading of current articles and the presentation of assigned topics.

> The Zoölogical Seminary met under the direction of Professor Brooks to read and discuss topics in Zoölogy and Animal Morphology.
>
> The chief topic for the year 1892-3 was the Echinoderms, in their anatomical, embryological, physiological and phylogenetic relations. At the beginning of the year the great classics on the Echinoderms, the most important recent memoirs, and the papers in the journals were brought together in the library of the biological laboratory, from the Peabody Library, the general library of the University, the library of the geological department, and from other sources.
>
> This literature was then assigned to the more advanced members of the seminary, and several months were spent in the preparation of the reports.
>
> In the meantime Professor Brooks gave a general introductory course of lectures on the Echinoderms, and the anatomy and embryology of illustrative types was studied in the laboratory.
>
> Early in January the courses of lectures by the members of the seminary upon the assigned topics was begun, and it was continued, three times a week until the Easter recess, and it consisted of from three to five lectures or reports upon each of the following subjects: the anatomy and general zoölogy of the Holothurians; the embryology of Holothurians; the physiology of Holothurians; the physiology of Asteroids and Ophiourans; the embryology of Asteroids; the anatomy and zoölogy of Echinoids; the anatomy of Crinoids; the anatomy and zoölogy of Ophiourans; the homologies and affinities of Echinoderms.
>
> Professor Uhler permitted us to keep in the laboratory, for the whole year, a number of memoirs from the Peabody Library, and the opportunity to study and compare them at our leisure contributed materially to the success of this course.
>
> In addition to this chief topic, Dohrn's memoir on the "Ursprung der Wirbelthiere" was read and discussed. Professor Brooks lectured on the evidence as to the origin of the vertebrates which is afforded by the Tunicates; and Prof. T. H. Morgan of Bryn Mawr College gave three lectures before the seminary on Balanoglossus, describing his own studies at the marine laboratory of the university, and discussing the evidence afforded by Balanoglossus, as to the origin of the Vertebrates.
>
> Korschelt and Heider on the embryology of Insects was also read and discussed by the seminary, and Professor Brooks gave three lectures on "Pelagic life in its relation to the evolution of the Metazoa," and four lectures on the affinities of Salpa.[87]

This rather lengthy abstract from the Johns Hopkins University, Report of the President gives a very accurate description of the character of the Seminary. The assigned readings provided the graduate students with the most current literature on the topic. Brooks was able to present an overview of the topic at the outset, while the students were preparing for their presentations. From Curtis's notes of the Seminary session on echinoderms, Brooks's treatment was in the classic systematic genre.[88] Each echinoderm group was described and characterized. Then, the phylogenetic relationships were presented, with the evidence from characteristics of the group.

Other topics were also discussed. From the epitome of the Seminary of 1892-1893, a major topic was the evidence for the origin of vertebrates from tunicate studies. By offering lectures on this topic, Brooks and T. H. Morgan (1866-1945) exposed the graduate students to one of the major questions facing morphology. The assignment and discussion of the works of Anton Dohrn and Eugen Korschelt (1858-1946) and Karl Heider (1856-1935) were important for much this same reason.

Subsequent years saw the Seminary offering a similar program. In addition to always including research topics upon assigned subjects, the following books were read and discussed: Arnold Lang, Lehrbuch der Vergleichenden Anatomie (1885); Louis Agassiz, "Essay on classification" (1857); Brooks, Fundamentals of Zoology (1899); E. B. Wilson, The Cell in Development and

Inheritance (1896); T. Jeffrey Parker and William A. Haswell, A Textbook of Zoology (1897); and Oscar Hertwig, Textbook of the Embryology of Man and Mammals (1892).[89]

The Journal Club and Morphological Seminary were not the sole source of exposure to the current literature. Brooks encouraged his students to read extensively in their own area of interest and to acquaint themselves generally in all areas of morphology. E. G. Conklin, a Ph.D. from Johns Hopkins in 1891, kept copious reading notes of the publications he read from 1889-1891. The list contained no less than seventy-three entries cataloged in seven volumes under "General reading notes," "Journal Reports," "Protozoa, Coelenterata, Echinodermata," "Mollusca, Echinodermata," "Vermes, Arthropoda," and "Chordata."[90] A perusal of the articles reveals the works of Ernst Haeckel, H. V. P. Wilson (1863-1939), E. Ray Lankester, Patrick Geddes (1854-1932), Oscar and Richard Hertwig, Adam Sedgwick (1785-1873), Hans Driesch, Elias Metschnikoff (1845-1916), A. S. Packard, C. Kupffer (1829-1902), C. Ishikawa (n.d.), E. B. Wilson, Karl Heider, Carl Rabl (1853-1917), Fr. Blochmann (1858- ?), O. Bütschli (n.d.), Hermann Fol (1845-1892), W. Salensky (1847-1918), Edward L. Mark, W. K. Brooks, E. Van Beneden (1809-1894), C. O. Whitman, Berthold Hatschek (1854- ?), Arnold Lang, C. Claus (1835-1899), A. Goette (1840-1922), Alexander Kowalewsky, William Bateson and Anton Dohrn. In short, Conklin's reading notes, which were exhaustive and often offered complete translations or abstracts of previously untranslated articles, included material from virtually every worker involved in late nineteenth-century morphological research. His notes were drawn from the list of works from Brooks's own reading assignments for his graduate students. This was a formidable list that was published as a "Course of reading for graduate and special students in morphology at the Johns Hopkins University."[91]

Perhaps of equal importance to Brooks's role as a teacher, laboratory instructor and literature guide, was his role as the director of the Chesapeake Zoological Laboratory (CZL), a transient adjunct to the Biology Department.[92] The importance of this institution was due to a number of factors.

As a marine laboratory established for research and instruction in marine biology, the CZL was the first of its kind in the United States when it opened in the summer of 1878.[93] Penikese had closed in 1874. Alexander Agassiz still maintained his private laboratory at Newport and the U. S. Fish Commission had its own laboratory. However, none of these was designed to encourage individual investigation of marine fauna and flora and, at the same time, to educate graduate students in research procedures. It was the desire to provide such a facility that prompted Brooks to suggest the idea to President Gilman.

> I wish to ask your opinion of the following proposition. I have been engaged for some years past in studying the development of the Mollusca, and have three papers on the subject now in the course of publication. As part of this work I wish, this summer to study the development of the oyster; a subject of practical importance apart from its scientific interest. Several of the students in the Biological Laboratory also wish to spend the summer in work of a similar character, and we ask that the

> University help us by paying the expenses of a laboratory, somewhere upon the Maryland coast, to accommodate about ten students. This laboratory would promote the researches of persons connected with the University; it would furnish facilities for other persons who wish to spend the summer vacation in studying zoology; it would promote the knowledge of the animal life of our waters, and it would furnish an opportunity to collect the material used during the year, for morphological teaching in the laboratory at the University. . .[94]

Apparently Brooks's proposal to establish the CZL convinced President Gilman. He authorized Brooks to begin work in the summer of 1878 at Fort Wool, Virginia. In addition, he convinced the trustees of the University to approve Brooks's incredibly modest request for $700 ($150 for rent, $100 for a boat, $250 for furniture and outfitting, $200 for preservative)[95] to prepare the laboratory.

With such a meager beginning, the CZL opened at the "incompleted fortification known as Fort Wool."[96] With a party of ten the first year, twelve the following year at Crisfield, Maryland and six in 1880 at Beaufort, North Carolina, the CZL had a notable impact upon the American zoological community. At least fifteen articles were published directly as the result of the summer work between 1878 and 1880. Several of these publications were in European journals. The fact that the CZL was well on its way to developing an international reputation by this time was supported by an article appearing in Nature, the English scientific journal. The article called upon the American people to support the CZL monetarily to allow Johns Hopkins to establish a permanent laboratory on the Chesapeake under the direction of Brooks. Dismissing the attempt at Penikese as a ". . . sort of holiday pic-nic of some weeks" the author continued to proclaim the CZL as the first seaside laboratory to be conducted by an university. Moreover, the initial years resulted in "good observations" by Brooks and his students on Lingula and several other molluscs. The author of the article was the English morphologist E. Ray Lankester.[97] According to a letter from Brooks to Gilman, other European "naturalists" had also communicated with him and conveyed their encouragement for both the CZL and the work being undertaken at the laboratory.[98]

Another important aspect of the CZL was its role as the training site for many of America's most able biologists of the late nineteenth and early twentieth centuries. Of the four objectives that Brooks cited in the "Report of the Chesapeake Zoological Laboratory" of 1878, two related directly to the training of students.

> 1. Furnish advanced students with opportunities for original investigations.
> 3. Enable less advanced students to become acquainted with diverse forms of life to be studied at seashore and to give them acquaintance with methods of marine zoological research.[99]

Initially, the CZL was to be a research opportunity for a "selected company of advanced students of zoölogy."[100] However, Brooks soon recognized the value of the training for all the graduate students in zoology.

> [The student] had the opportunity of laying a broad foundation for his future work as a naturalist, of finding for himself some matters to investigate, and thus early to acquire the mental habit of the independent investigator.[101]

Therefore in the early 1880's Brooks required that all of his students have "At least two months' study at the marine laboratory of the University between June 1st and August 31st."[102]

From all indications available, Brooks's students did not suffer under the requirement for marine study. There are a number of warm, humorous and attractive anecdotal stories that relate various activities of the summer sessions of the CZL.[103] E. G. Conklin noted that the laboratories provided the means for the establishment of the warm feelings that characterized Brooks's relationships with his students.

> It was on these expeditions that his students came to know him most intimately and affectionately. In the memory of each of them is fixed some scene of his [Brooks] enthusiasm over the discovery of a rare form or of an unknown stage in some life history; his long vigils full of exciting discoveries; his quiet talks on nature and philosophy.[104]

Furthermore, the students at Johns Hopkins clearly realized the value of the training they received at the CZL for their own professional development. Due to monetary problems of the University, the CZL was not opened as an independent entity from 1888 to 1890. Brooks did arrange, however, for the students to use the U. S. Fish Commission Laboratory at Woods Hole and the Marine Biological Laboratory. For many reasons, several of the students objected to this arrangement, favoring instead the re-establishment of the CZL in a location further south.[105] In a letter to President Gilman to which Brooks appended a letter of approval and support, the students detailed their reasons for desiring that the CZL be established for the summer of 1891.

> Embryological work, the most important seaside work, is carried on under great disadvantage in a cold climate. . . . The fauna of warm seas is not only very rich, varied and accessible, but

> offers a much greater proportion of such forms as promise aid in solving the important morphological problems of to-day. It was this which led Naturalists to visit Naples long before any permanent Laboratories had been erected there.[106]

The request was granted and, once again, Johns Hopkins funded the summer biology laboratory.

The work Brooks's students conducted at the CZL offers another parameter by which to measure the value of the laboratory upon the development of American biology. Most of the investigations involved morphological descriptions of the developmental stages of selected marine invertebrates. The emphasis upon embryological studies is understandable, given the prevailing attitude of the role that such work had upon the major morphological studies. Furthermore, the selected invertebrate for study was usually due to that organism's value in looking at a specific problem of morphology. For example, Brooks encouraged that one of the students at the CZL investigate Amphioxus.

> Amphioxus is a small worm-like animal, the lowest of the Vertebrates, and it is of very great scientific interest since it has preserved many evidences of a relationship to various groups of invertebrates, and thus serves to bridge over the gap which was supposed by Cuvier and Agassiz to separate the Vertebrates from all lower forms of life. Its embryology which may be termed the key to the embryology of all the higher animals, has been ably studied by several of the most distinguished Zoologists of Europe, and a number of papers have appeared upon the subject within a few years.[107]

Most of the studies had a similar bearing upon questions of equal importance to that of the Amphioxus work. The laboratory at Beaufort, the most frequent location of the CZL, offered the best opportunity for studying many of the desired organisms. Since it was protected by Cape Hatteras, the flora and fauna of Beaufort was different from that found in the northern areas of the Atlantic. In addition to its uniqueness, the area was exceedingly rich in animal life. From the surrounding sand bars, mud flats, salt marshes and protected sounds, Brooks was able to procure abundant supplies of Amphioxus, Renilla, Limulus, Balanoglossus, various echinoids, a wide variety of annelids, assorted polyps, molluscs and crustaceans.[108]

The method of instruction at the CZL under Brooks mirrored the same approach he used in the Laboratory in Baltimore. Despite the fact that the early sessions included many students who were neither well-versed in zoology or competent researchers, Brooks generally left them to develop on their own. He did provide the necessary library sources, collecting trips and laboratory facilities as well as serving as a resource person when the student requested aid. The following account is Brooks's own from the initial session of the CZL in 1878.

> No lectures were given, as the needs of the different members of the class were too diverse to make lectures advantageous.
>
> Each student had access to the library, and the proper reading to be done in connection with the study of each form of life was pointed out by the Associate in charge [Brooks]. They had the benefit of all the distant excursions which we were able to make, and were thus enabled to become familiar with the methods of deep-water collecting; and there was at least one surface-collecting excursion every day of the season, and more than one on every favorable day.
>
> There were several shore-collecting expeditions, and both sides of Hampton Roads were visited and examined. In these ways the students were able to acquire familiarity with the habits of marine animals while gathering the material for laboratory work.

> In the laboratory, each student had ample room for dissecting and for microscope work, as well as all the necessary facilities for keeping and observing living animals in aquaria. Only one of the students, during the past summer, had ever done any work in marine zoology before, but if the laboratory should be continued, several of the class would be able to take up subjects for original investigation next year.[109]

The method proved successful in the first year. This provided the model for all the subsequent sessions of the CZL.[110]

Several investigations that students of the CZL accomplished during the summer session became widely recognized as important studies and, in this manner, increased the prestige of the entire program. H. W. Conn (1859-1917) published work from the summers of 1882-1883 under the title "On radial and bilateral symmetry in animals," and his paper,"Development of *Thallasima*" received the Walker Prize for excellence from the Boston Society of Natural History. E. B. Wilson's monumental work, "The development of *Renilla*," was the result of several summers at the CZL beginning in 1879. The work was recognized in Europe.

> Dr. Wilson writes from Naples that his work at Beaufort on Renilla was so favorably received that Dr. Dohrn, the Director of the Naples Laboratory has invited him to prepare the report on this group of animals for his magnificent publication "The Fauna and Flora of the Gulf of Naples." . . . The fact that the opportunity has been offered to him shows, though, I think, that our men can hold their own among the Naturalists of Europe.[111]

William Bateson came to Beaufort to work under Brooks specifically on the developmental stages of *Balanoglossus*, another organism with features having application to the questions surrounding vertebrate ancestry. Bateson published this work as "The early stages in the development of Balanoglossus" and continued to work on the organisms throughout the 1880's. The work represents a classical example of morphological investigation. E. A. Andrews (1859- ?) conducted several investigations of the developmental histories of selected annelids. Much of this work served as the basic material for cell-lineage studies of the 1880's. H. V. P. Wilson was successful in tracing the development of selected polyps from the egg to the adult. His work represented some of the earliest and most complete studies of polyps. From 1885-1887, F. H. Herrick conducted an exhaustive study of the embryology, anatomy, systematic zoology and habits of the crustacean genus, Alpheus. The work was included in a joint publication by Brooks and Herrick in 1892, "The embryology and metamorphosis of the Macroura."

The CZL also offered the opportunity for many of Brooks's students to select a research topic to work on for their doctoral degree. Many of the students used the required attendance at one or more of the summer sessions to conduct their research. Over thirty of Brooks's Ph.D. students presented work from the CZL for their dissertations.[112] Many of these works were important and widely recognized as valuable additions to zoological literature. A few examples include the following: E. B. Wilson, "The origin and significance of the metamorphosis of Actinotrocha"[113]; Thomas H. Morgan, "A contribution to the embryology and phylogeny of the pycnogonids"[114]; E. G. Conklin, "The embryology of Crepidula"[115]; Ross G. Harrison (1870-1959), "The development of the median and paired fins of teleosts"[116]; George Lefevre (1869-1923), "Budding in Perophora"[117]; R. P. Cowles (1872-1948), "Phoronis architecta"[118]; and David Hilt Tennent (1873-1941), "A study of the life history of Bucephalus haimaenus, a parasite of the oyster."[119]

The work of the students and their publication record from the investigations undertaken at the CZL was a source of great pride for Brooks. Not only was the quality of the work impressive and the number of publications notable, but the national and international scope of the articles provides some idea of the growing reputation of the CZL. Brooks made a conscious effort to point out that by 1883 work from the CZL had resulted in over fifty-five papers published in Studies from the Biological Laboratory of Johns Hopkins University, Johns Hopkins University Circulars, American Naturalist, American Journal of Science, Memoirs of the Boston Society of Natural History, Zoölogischer Anzeiger, Quarterly Journal of Microscopical Science and Proceedings and Philosophical Transactions of the Royal Society.[120] Subsequent work served to increase the publication list.

The CZL was also the focus of Brooks's own research.[121] In his initial request to President Gilman, Brooks mentioned the desirability of a seaside laboratory "to study the development of the Oyster; a subject of practical importance apart from its scientific interest."[122] Brooks continued this work during several summers after 1878 with the active encouragement of the administration of Johns Hopkins. At the time the Chesapeake oyster industry was facing a critical period.[123] Problems with pollution, over-harvesting, poor recruitment and decreasing quality of the oyster were of major concern. Brooks's research clearly established him as the leading American expert on the oyster. As a result, he was appointed to the commission to study these problems in 1882. Brooks efficiently used the CZL and several of his students to work on these problems during several of the summer sessions.

Another ongoing interest of Brooks at the CZL was "to promote the knowledge of animal life" in the Chesapeake Bay area specifically and in the marine environment in general.[124] Coupled with his desire to address the major morphological problems of the day, much of Brooks's research can be understood as being directed in this manner. His work of the genus Salpa and other tunicates was the offshoot of work he began at Newport with Alexander Agassiz. The studies had important implications for the theory of the origin of vertebrates and the origin of pelagic life. The tunicates were actively studied by Brooks throughout the 1880's. Another subject that occupied Brooks for his entire career was work on the larval stages of various Crustacea. He was interested in being able to demonstrate the ubiquitous nature of the nauplius stage in the larval history of many crustaceans. This could shed information about the common ancestry of the entire group through a nauplius-like ancestor. Limulus, an arthropod, was another favorite organism for study. Since it shared many characteristics of extinct arthropods, Brooks viewed investigations of its development as particularly important for the phylogeny of the entire arthropod phylum. Brooks's interest in hydromedusae, a subject of many of his studies in Beaufort and the Bahamas, dated from his association with John McCrady. These organisms presented the investigator with several interesting questions: a complicated and varied life history; relationships to Haeckel's Gastrae theory; easily observable anatomical structures; and their possible role in questions concerning the formation of the pelagic fauna. Brooks was interested in all these facets of hydromedusae research and contributed impressively to each.

Brooks's position as an original member of the faculty in the first graduate department of biology in America and his role in developing the first seaside laboratory for advanced zoological research in the United States, illustrates some of the influence he had over the direction American biology took in the late nineteenth century. Another measure of his status is obtained by examining the biologists who studied under Brooks. Of the forty-three students who received doctorates as a direct result of Brooks's supervision, the overwhelming majority went on to positions of importance in many of America's leading institutions. The biology departments of Williams College, Columbia University, Wesleyan University, Johns Hopkins University, University of North Carolina, University of Maine, Princeton University, Massachusetts Institute of Technology, Oberlin College, Yale University, University of Missouri, Harvard University, University of Minnesota, West Virginia University,

University of Vermont, University of Michigan, Bryn Mawr and St. John's College all contained faculty members who had received their Ph.D. from Brooks at Johns Hopkins. Among these men were S. F. Clarke (1851-1928), E. B. Wilson, E. A. Andrews, Henry V. P. Wilson, T. H. Morgan, E. G. Conklin, R. P. Bigelow (1863-1955), Ross G. Harrison, H. L. Clark (1870-1947), R. P. Cowles and David H. Tennent.[125] Morgan eventually was awarded the Nobel Prize in 1933 and Harrison was nominated for the award by the Nobel Prize committee.

In Brooks's tenure at Johns Hopkins, the role of morphology gradually increased in importance, especially when compared with the early days of the department. Since the time when Brooks was appointed as "Associate in Zoölogy" as Martin's assistant, morphology became one of the major thrusts of the department. From 1876-1893, when Ph.D.'s in the department were listed in physiology under Martin and in zoology under Brooks, there were eighteen degrees given in physiology and nineteen in zoology. While the number of degrees was similar, it must be remembered that the morphology program was not well established at the inception of the department while physiology was provided for. The growth of morphology became marked later. Between 1893 and 1908, twenty-four doctorates, all descriptive morphology, were awarded in zoology while only nine were given for work in animal physiology during the same time. Much of the success of morphology at Johns Hopkins can be directly attributed to Brooks's development of a successful instructional program and the development of the marine program through the CZL.

The success of Brooks in the department did not escape the notice of the administration. In 1883 he was raised in academic rank to the recently instituted position of Associate Professor in Comparative Anatomy. The title changed later to Associate in Morphology. By 1891, he had been promoted again, this time to Professor of Animal Morphology. When Dr. Martin resigned from the department in 1893, Brooks was appointed as Head of the Biological Laboratory, a position he held until his death in 1908. Brooks's title changed twice more in the last ten years of his career, to Professor of Zoölogy and finally to Henry Walters Professor of Zoölogy.

Brooks entire professional life was spent at Johns Hopkins. It is not surprising, consequently, that his family life had its origin in Baltimore. Shortly after his appointment to the faculty in 1876, he met Amelia Katharine Schultz (n.d.-1901), the daughter of Edward and Susan Schultz of Baltimore. Her family lived near "Brightside" on Lake Rowland where many of the other members of the Biology Department lived.[126] It was here that Brooks and Katharine met and courted. They were married on June 13, 1878.

The original family home of the Brooks family was in Baltimore. However, a bequest from Mrs. Posey, an aunt of Mrs. Brooks, gave the beautiful home of "Brightside" to the Brooks. It proved to be a most beneficial gift, for it was here that Brooks was able to pursue his other avocation, gardening and plant hybridization. The home was located on a generous plot of land. There was a large garden, many trees and greenhouses in which Brooks raised his flowers, especially his own varieties of orchids. The home also served as the frequent gathering spot for graduate students. On many occasions the Journal Club or the Seminary would meet at "Brightside" for discussions.

Brooks and his wife had two children. The eldest, Charles Ernest (1879-1935) eventually earned his doctorate in mathematics from Johns Hopkins and joined the faculty at the University of Wisconsin as a statistician. The youngest child was a girl, Menetta White (1881-1972). She was educated at Vassar College, returned to Baltimore in 1901 and married a graduate student of Brooks, J. Franklin Daniel.[127] Brooks was extremely devoted to his family. During several of the summer sessions of the CZL, he packed up the entire clan and took them to the laboratory site. However, in 1881 the recent birth of Menetta and the subsequent weakness of Katharine Brooks made this practice not possible. In a letter to President Gilman, Brooks revealed the attachment he had to his family by relating his loneliness from being separated from them.

> I do not think I ever knew what homesickness was until this summer but as I have pulled through three months I suppose I can stand another, although I count the days. Fortunately Mrs. Brooks is unusually well this summer and sends me a letter by every mail.[128]

Mrs. Brooks's health did not continue to improve. In the early 1890's she became so ill that Brooks felt compelled to withdraw from the directorship of the CZL to care for her. In 1892, E. A. Andrews was acting director and in 1893, R. P. Bigelow served in that capacity. Her condition improved sufficiently in 1894 that Brooks again served as Director for the laboratory work. However, this was the last year that Brooks was able to spend the entire summer at the marine laboratory until after 1901. It was in this year that Katharine died after spending almost the last decade of her life as an invalid, tenderly cared for by Brooks.

Following the death of her mother, Menetta moved back to Baltimore. She assumed control over the home at "Brightside," was the unofficial hostess at the many social gatherings at the home and provided much comfort to her father. By 1902, Brooks had recovered from the loss of his wife sufficiently to invite again the graduate reading groups to his home. These sessions continued through the early years of the twentieth century. But, Brooks's own health began to fail significantly in 1906. The congenital heart defect that often caused him to restrict his activities was beginning to take its toll.

Brooks had informed E. G. Conklin that he planned to retire when he reached sixty years of age (March 1908) and then devote himself completely to philosophical and scientific work.[129] This desire was never fulfilled.

> In 1908 difficulty in breathing added to his burdens and his machinery was most seriously out of order. He continued to come to his lectures and work earnestly to complete a final paper on salpa, for which the drawings were finished and which he planned to write out in the summer. This, he said, would probably be his last piece of serious microscopic research,

> since trouble with his eyes made the employment of immersion lenses too difficult; and his mind was eager to digest the facts of his long experience and the recent work of others. But his strength was not equal to the task. Sudden attack confined him to his home, but yet his will brought him back to the laboratory, till one last day, February 12. After preparatory rest, driven by his consciousness, he forced himself to attend an oral examination of a candidate for the degree of Ph.D. Then walking to the train that brought him home, he was there overcome by a serious collapse. He was persuaded to go to the hospital and, after most severe attacks there, rallied; but in nine long months that followed he scarcely left his wheel-chair.[130]

On November 12, 1908, William Keith Brooks died at his home in "Brightside" following cardiac and renal failure.

NOTES

CHAPTER TWO

1. The biographical sources on Brooks are quite limited. Most were written by his students and colleagues at Johns Hopkins University. The available sources include: E. A. Andrews, "Sketch of William Keith Brooks," Popular Science Monthly 55 (1899), pp. 400-409; E. A. Andrews, "William Keith Brooks," Science 28 (1908), pp. 777-786; E. A. Andrews, "William Keith Brooks," in Leading American Men of Science, ed. by David Starr Jordan (New York: Henry Holt and Company, 1910), pp. 427-455; R. P. Bigelow, "William Keith Brooks (1848-1908), Obituary," Proceedings of the American Academy of Arts and Sciences 71 (1937), pp. 489-492; E. G. Conklin, "Biographical Memoir of William Keith Brooks, 1848-1908," National Academy of Sciences, Biographical Memoirs 7 (1913), pp. 23-88; E. G. Conklin, "The Life and Work of William Keith Brooks," Anatomical Record 3 (1909), pp. 1-15; E. G. Conklin, "William Keith Brooks," Proceedings of the American Philosophical Society 47 (1908), pp. iii-x; M. V. Edds, Jr., "Brooks, William Keith," Dictionary of Scientific Biography, ed. by Charles C. Gillespie (New York: Charles Scribner's Sons, 1970), Vol. II, pp. 501-502; Dennis M. McCullough, "W. K. Brooks's Role in the History of American Biology," Journal of the History of Biology 2 (1969), pp. 411-438; and "William Keith Brooks. A Sketch of His Life by Some of His Former Pupils and Associates," Journal of Experimental Zoology 9 (1910), pp. 1-52. The best of the sources are Andrews' article in Leading American Men of Science and Conklin's memoir in the National Academy of Sciences, Biographical Memoirs. In addition, the memorial volume of the Journal of Experimental Zoology contains several personal accounts of Brooks's personality and teaching style as interpreted by former students and colleagues (S. F. Clarke, W. Bateson, H. V. P. Wilson, H. McE. Knower, G. Lefevre, O. C. Glaser, A. G. Mayer, E. G. Conklin, M. M. Metcalf, F. H. Herrick, G. G. Drew, G. Graver and H. H. Donaldson.

2. The eldest son, Oliver Kingsley, was born in 1845. Following Brooks's birth in 1848 were Charles Ernest (1851) and Edward Howard (1854). Brooks appeared to be closest to Oliver, maintaining a correspondence with him throughout his lifetime. Oliver provided one of the major resources for material concerning Brooks's early years. He was an executive with National Malleable Casting Company. Charles remained a bachelor until shortly before his death. He, too, was employed by National Malleable. Brooks honored his younger brother by naming his own son after him. The youngest brother, Edward,

became an interior decorator and furniture maker of notable repute. All the Brooks brothers, with the exception of William Keith, spent their lives in the vicinity of Cleveland.

3. The Brooks were second cousins through the Keith family. Oliver's ancestors came from England prior to 1634 (Thomas Brooks) and Ellenora's relatives settled in Dorchester, Massachusetts from England around 1638.

4. The information is from "Early History of W. K. Brooks" by Oliver K. Brooks. It was printed in complete form in Conklin's memoir in the National Academy of Sciences, Biographical Memoir.

5. J. G. Wood, The Illustrated Natural History (London: George Routledge and Sons, 1858). The book, inscribed to "Willie K. Brooks," is now in the possession of Amasa B. Ford, Brooks's grandnephew.

6. Ibid., p. 233.

7. The subject of many of these excursions was the investigation of Indian mounds and artifacts. This may explain Brooks's interest in Indian culture that led to the publication on the Lucayan Indians later in his life. ("The Lucayan Indians," Popular Science Monthly 36 (1880), pp. 88-98; "On the Lucayan Indians," Memoirs of the National Academy of Science 4 (1889), pp. 213-222.

8. Jared Potter Kirtland (1793-1877) was a naturalist who became well known in Ohio for his ornithological and piscine work. His inspiration led several of his pupils, most notably Brooks and Comstock, to form the Kirtland Society of Natural Science (Cleveland).

9. The essay prize was awarded to the student who produced the best essay during the year. Brooks's achievement to win the prize as a freshman was recognized as remarkable.

10. William Keith Brooks, Foundations of Zoology (New York: The Macmillan Company, 1899), frontispiece.

11. Sanborn Tenney published one of the earliest American natural history texts (Natural History. A Manual of Zoology [New York: Charles Scribners, 1865]). He later went on to teach at Vassar College.

12. One excursion, which Brooks did not participate in, included a noteworthy natural history expedition across South America.

13. Comments of T. H. Brooks (no relation) included in E. G. Conklin, "William Keith Brooks," National Academy of Sciences, Biographical Memoirs, p. 35.

14. Ibid., p. 34.

15. Ibid., p. 35.

16. Burt G. Wilder, "Agassiz at Penikese," American Naturalist 33 (1898), p. 189.

17. David Starr Jordan, "Agassiz at Penikese," Popular Science Monthly 40 (1892), p. 722.

18. Letter, Louis Agassiz to W. K. Brooks, March 20, 1873, American Philosophical Society Library, Manuscript Collection, Miscellaneous files.

19. David Star Jordan, "Agassiz at Penikese," p. 723.

20. The inclusion of a substantial number of women is often cited as proof of Agassiz's belief in equal education for both sexes. Unfortunately this ideal did not become a standard practice in American higher education following Penikese.

21. "Penikese Island," Harpers Weekly, August 9, 1873, pp. 701-702.

22. Ibid., p. 701.

23. This same sign is placed in the lobby outside the Library at the Marine Biological Laboratory in Woods Hole.

24. David Starr Jordan, "Agassiz at Penikese," p. 725-726.

25. E. L. Mark, "Zoology," in The Development of Harvard University since the Inauguration of President Eliot, ed. by Samuel Eliot Morrison (Cambridge: Harvard University Press, 1930), p. 383. The instructional crisis that resulted from Agassiz's death in 1873 was compounded by T. H. Huxley's refusal of the offer to be the successor to Agassiz. The offer was made repeatedly. Finally, faced with John McCrady's failing health and a decreased number of students, something had to be done. In 1877, the advanced course in zoology was dropped and the introductory course was divided between Walter Faxon and E. L. Mark, both recent Ph.D.'s with little teaching experience. Laboratory work, the main thrust of European programs, was dropped by the zoologists and was not implemented again until 1880. There was some laboratory work that was conducted in the MCZ under Alexander Agassiz's guidance. However, it was only offered on an unofficial basis for fourth-year students in the Lawrence Scientific School in 1880-1881 and, two years

later, in the Natural History program open to other college students. This situation created a serious problem for Harvard to offer a quality program in harmony with European programs. For this reason, it is not surprising to note that most American graduate students in biology preferred to study in Europe or to attend the Biology Department at Johns Hopkins University. Mark, himself, obtained his degree in Leipzig and Faxon spent some time in Europe learning micro-technique.

26. Ibid., p. 383. Brooks was awarded the first Ph.D. in zoology from Harvard and one of the earliest advanced degrees ever awarded from that institution. The first Ph.D. awarded was in mathematics to William Elwood Byerly (1873). The other Ph.D.'s in zoology were to Edward A. Birge (later president of University of Wisconsin), J. W. Fewkes (later chief of the Bureau of American Ethnology) and Walter Faxon (Professor of Zoology at Harvard).

27. W. K. Brooks, "On an Organ of Special Sense in the Lamellibranchiate Genus Yoldia," Proceedings of the American Association for the Advancement of Science 23 (1875), pp. 80-82.

28. W. K. Brooks, "Embryology of the Fresh-Water Mussel," Proceedings of the American Association for the Advancement of Science 24B (1876), pp. 238-240.

29. Letters: A. S. Packard to D. C. Gilman, May 27, 1876, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection; E. S. Morse to D. C. Gilman, May 26, 1876, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection; Alpheus Hyatt to W. K. Brooks, May 27, 1876, Johns Hopkins University, Eisenhower Library Manuscript Room, Miscellaneous collection.

30. W. K. Brooks, "Embryology of Salpa," Proceedings of the Boston Society of Natural History 18 (1875), pp. 193-200.

31. Letter, A. S. Packard to D. C. Gilman, May 27, 1876.

32. E. G. Conklin, "Biographical Memoir of William Keith Brooks," p. 39.

33. Ibid., p. 39.

34. T. B. Comstock, "Discussion and Correspondence: William Keith Brooks," Science 29 (1909), pp. 614-616.

35. Gilman was a most interesting man and certainly exerted a powerful influence over American higher education. Of the literature on Gilman, the two best are: Francesco Cordasco,

The Shaping of American Graduate Education. Daniel Coit Gilman and the Protean Ph.D. (Tolowa, New Jersey: Rowman and Littlefield, 1973); Abraham Flexner, Daniel Coit Gilman, Creator of the American Type of University (New York: Harcourt, Brace and Company, 1946).

36. Abraham Flexner, Daniel Coit Gilman, p. 78. (Letter from Alexander Agassiz to D. C. Gilman, March 23, 1876.)

37. Letter, W. K. Brooks to D. C. Gilman, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

38. Letter, W. K. Brooks to D. C. Gilman, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

39. Letter, John McCrady to D. C. Gilman, May 27, 1876, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

40. Letter, Alpheus Hyatt to W. K. Brooks, May 27, 1876.

41. Ibid.

42. Letter, E. S. Morse to D. C. Gilman, May 26, 1876.

43. Letter, A. S. Packard to D. C. Gilman, May 27, 1876.

44. Letter, W. K. Brooks to D. C. Gilman, June 13, 1876, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

45. "Preliminary Announcement," Johns Hopkins University, Report of the President (January 17, 1876), p. 30.

46. E. L. Mark, "Zoology," p. 384.

47. Martin and Huxley had even collaborated on producing a text-book. Huxley sent Gilman a copy for his examination.

48. R. P. Cowles, "The Department of Biology, Johns Hopkins University" (unpublished manuscript, Johns Hopkins University, Eisenhower Library Manuscript Room), p. 15. Letter from D. C. Gilman to T. H. Huxley, March 14, 1876.

49. Ibid. Letter from D. C. Gilman to H. Newell Martin, March 14, 1876.

50. Hugh Hawkins, Pioneer: A History of the Johns Hopkins University 1876-1889 (Ithaca, New York: Cornell University Press, 1960), pp. 48-49.

51. Gilman had offered Martin $2500 per annum. Martin requested and was given $4000 per year for two years and $5000 yearly after that.

52. Letter, W. K. Brooks to P. R. Uhler, June 18, 1876, Johns Hopkins University, Eisenhower Library Manuscript Room, Miscellaneous collection.

53. H. Newell Martin, "The Study and Teaching of Biology," Popular Science Monthly 10 (1877), p. 300.

54. Ibid., pp. 308-309.

55. R. P. Cowles, "The Department of Biology," pp. 18-19.

56. Hugh Hawkins, Pioneer, p. 71.

57. This is not to suggest that Martin and Brooks were ever involved in conflict between their respective disciplines or competition for students. It is meant to suggest that the morphological program developed by Brooks was sufficiently attractive to obtain students in a department where medical physiology received initial favor.

58. Work by S. F. Clarke. This was one of the first doctorates awarded by the Biology Department in 1879.

59. "Biological Laboratory," Johns Hopkins University, President's Report (1878), pp. 16-17.

60. Letter, W. K. Brooks to Johns Hopkins University Trustees, June, 1878, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

61. 1893 was the target date for the beginning of the medical school and hospital.

62. See note #25.

63. "Biological Laboratory," Johns Hopkins University, Report of the President (1879), p. 53. In addition, Brooks taught a course entitled "Teacher's Class in Zoology" patterned after his experience at Penikese. Faced with no laboratory manual, he developed his own. This became popular outside of Johns Hopkins as both Alpheus Hyatt (Boston Society of Natural History) and Walter Faxon (Harvard) began to use it. Brooks expanded the manual and published the Handbook of Invertebrate Zoology (Boston: Cassino, 1882), recognized as the best laboratory manual available.

64. E. G. Conklin papers, "General Zoology notes November 6, 1888-April 9, 1889," Princeton University, Firestone Library, Manuscript Room.

65. Ibid.

66. "William Keith Brooks," Journal of Experimental Zoology 9, p. 14.

67. "Biological Laboratory," Johns Hopkins University, Report of the President (1879), p. 62.

68. "William Keith Brooks," Journal of Experimental Zoology 9, pp. 14-15.

69. E. G. Conklin, "Biographical Memoir of William Keith Brooks," p. 44.

70. "Biology," Johns Hopkins University, Circulars (1885), p. 95. The instructors available during 1885 were Andrews, McMurrich, Bruce, Lugger and Dr. Brooks. Andrews, McMurrich and Bruce were all advanced graduate students who served as teaching fellows or laboratory assistants.

71. A detailed examination of this work is undertaken in Chapter Three.

72. E. A. Andrews, "Sketch of William Keith Brooks," p. 404.

73. In 1893, H. Newell Martin retired from the Biological Laboratory for health reasons. Brooks was appointed as head of the department and the Journal of Morphology began publication. Any or all of these factors may have played a role in the discontinuance of Studies from the Biological Laboratory.

74. The Journal of Experimental Zoology was founded by several of Brooks's former graduate students. Ross G. Harrison (1894) was the managing editor. Other Johns Hopkins' products included E. G. Conklin (1891), Thomas H. Morgan (1890) and E. B. Wilson (1881). The remainder of the editorial board consisted of W. E. Castle, C. B. Davenport, H. S. Jennings, F. R. Lillie, Jacques Loeb, G. H. Parker and C. O. Whitman. The journal was founded to complement the Journal of Morphology (1887) by providing a specialized journal for research utilizing an experimental approach. The only other journal available in the United States was Science, and the articles published in this periodical tended to be more general and of a fairly brief nature. The American Naturalist was also published at this time. It too, however, was of a more general nature.

75. Brooks's correspondence from Beaufort in the summer of 1880 to D. C. Gilman provides support for this claim.

76. Letter, W. K. Brooks to D. C. Gilman, June 4, 1881, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

77. "Biology," Johns Hopkins University, Circulars (1883), p. 9.

78. R. P. Cowles, "The Department of Biology," p. 334. Translations of foreign work were also provided.

79. Winterton Conway Curtis papers, "Journal Club," University of Missouri, Elmer Ellis Library, Western Historical Manuscript Collection.

80. Otto Maas, "Bau und Entwicklung der Cuninenknospen," Zoölogische Jahrbücher: Abtheilung für Anatomie und Ontogenie der Tiere 5 (1891-92), pp. 271-300. The paper had references to work by Brooks, McCrady, and H. V. Wilson.

81. The paper was published in Zeitschrift für Wissenschaft Zoologie in 1892 but was not translated.

82. Paper available but not translated in Zeitschrift für Wissenschaft Zoologie.

83. William Bateson, "On Some Cases of Variation in Secondary Sexual Characters, Statistically Examined," Proceedings of the Zoological Society of London (1892), pp. 585-594.

84. The fundamental conceptions of life were, (1) life is response to the order of nature and, (2) the purpose of the response is for the good of the species.

85. R. P. Cowles, "The Development of Biology," p. 35.

86. "Biology Department," Johns Hopkins University, Circulars 6 (1887), p. 100.

87. "Biological Laboratory," Johns Hopkins University, Report of the President (1893), pp. 36-37.

88. Winterton Conway Curtis papers, Morphological Seminary (October 26-December 12, 1893), "Introductory Lectures to the Study of Echinoderms."

89. "Biological Laboratory," Johns Hopkins University, Report of President (1894-1907).

90. E. G. Conklin papers, "General reading notes," Princeton University, Firestone Library Manuscripts, Manuscript Room.

91. W. K. Brooks, "Course of Reading for Graduate and Special Students in Morphology at the Johns Hopkins University," Johns Hopkins University, Circulars 9 (1890, p. 37. There is marked correspondence between Brooks's list and Conklin's notes. Brooks divided his reading list into a "General Works" and "Special Works" section. The included works were: F. M. Balfour, A Treatise on Comparative Embryology; Charles Darwin, Origin of Species; Ernst Haeckel, Generelle Morphologie; A. R. Wallace, The Geographical Distribution of Animals; August Weismann, Essays on Heredity and Kindred Biological Problems; works of Adam Sedgwick on metameric segmentation; Metschirikoff's studies on germ layers; the Balanoglossus work of Bateson; papers by Brooks, Seeliger and Kowalewsky on tunicates; numerous selected papers on various groups of Arthropoda; and the latest research of Balfour, Dohrn, Hatschek, Hertwig, Huxley, and Lankester concerning vertebrate ancestry. Certainly a graduate student who had read this list would be well acquainted with current morphological issues.

92. The station opened in 1878 at Fort Wool, Virginia. It was later located at Crisfield, Maryland (1879); Beaufort, North Carolina (1880-1882, 1884-85, 1894-95, 1898-); Hampton, Virginia (1883); Green Turtle Key, Bahamas (1886); Nassau, Bahamas (1887); Woods Hole (1888-1890), Kingston, Jamaica (1891, 1893, 1896); Alice Town, North Bimini, Bahamas (1892); and Port Antonio, Jamaica (1897). A narrative history of the CZL was written by C. D. Seligson, "The Chesapeake Zoological Laboratory, 1878-1906," (unpublished paper, Johns Hopkins University, 1975). Other sketchy accounts are available in Johns Hopkins University, President's Reports, John C. French, A History of the University Founded by Johns Hopkins (Baltimore: The Johns Hopkins University Press, 1946) and "William Keith Brooks," Journal of Experimental Zoology 9.

93. This statement is correct when it is emphasized that the CZL was established exclusively for graduate work and research.

94. Letter, W. K. Brooks to D. C. Gilman, 1878, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

95. Ibid.

96. "Chesapeake Zoological Laboratory," Johns Hopkins University Report of the President (1878), p. 50.

97. E. Ray Lankester, "An American Seaside Laboratory," Nature 21 (1880), pp. 497-499.

98. Letter, W. K. Brooks to D. C. Gilman, May 15, 1882, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

99. Letter, W. K. Brooks to D. C. Gilman, 1878.

100. "Chesapeake Zoological Laboratory," Johns Hopkins University, Report of the President (1879), p. 32.

101. "William Keith Brooks," Journal of Experimental Zoology 9, p. 19.

102. "Biology," Johns Hopkins University, Circulars 3 (1884), p. 9.

103. Many of these anecdotes are contained in the Brooks memorial volume of the Journal of Experimental Zoology. Another source is R. P. Cowles unpublished manuscript, "The Department of Biology." A final source comes from the D. C. Gilman collection at the Eisenhower Library Manuscript Room (Johns Hopkins University). Of special worth are the letters from S. F. Clarke to Gilman written during the summer of 1879. Brooks's correspondence with Gilman contains several anecdotes. Other students related incidents to President Gilman.

104. "William Keith Brooks," Journal of Experimental Zoology 9, p. 19.

105. The committee was directed by E. A. Andrews and consisted of T. H. Morgan, R. P. Bigelow, E. G. Conklin, G. W. Field and R. G. Harrison.

106. Letter, E. A. Andrews to D. C. Gilman, December 1890, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

107. Letter, W. K. Brooks to D. C. Gilman, 1878.

108. "Chesapeake Zoological Laboratory," Johns Hopkins University, Report of the President (1883), p. 81.

109. "Chesapeake Zoological Laboratory," Johns Hopkins University, Report of the President (1878), p. 53.

110. The model included the concern for the whole organism in its natural habitat. This organismic approach to biological investigation was a trademark of the CZL.

111. Letter, W. K. Brooks to George W. Dobbin, July 15, 1883, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

112. Of Brooks's forty-three students, only ten wrote dissertations on subjects or organisms not directly involved with marine work.

113. E. B. Wilson, "The Origin and Significance of the Metamorphosis of Actinotrocha," Quarterly Journal of Microscopical Science 21 (1881), pp. 202-218.

114. Thomas H. Morgan, "A Contribution to the Embryology and Phylogeny of the Pycnogonids," Johns Hopkins University, Studies from the Biological Laboratory 5 (1891), pp. 1-76.

115. E. G. Conklin, "The Embryology of Crepidula," Journal of Morphology 13 (1897), pp. 1-54.

116. Ross G. Harrison, "The Development of the Median and Paired Fins of Teleosts," Archiv für Mikroskopische Anatomie und Entwicklungsmechanik 46 (1895), pp. 500-578.

117. George Lefevre, "Budding in Perophora," Journal of Morphology 14 (1898), pp. 367-424.

118. R. P. Cowles and W. K. Brooks, "Phoroms architecta: Its Life History, Anatomy and Breeding Habits," Memoirs of the National Academy of Sciences 10 (1905), pp. 71-148.

119. David Hilt Tennent, "A Study of the Life History of Bucephalus haimaenus, a Parasite of the Oyster," Quarterly Journal of Microscopical Science 49 (1895), p. 86.

120. "Chesapeake Zoological Laboratory," Johns Hopkins University, Report of the President (1883), p. 86.

121. This subject will be dealt with in detail in Chapter Three.

122. Letter, W. K. Brooks to D. C. Gilman, 1878.

123. Several newspaper accounts of the oyster problem and possible means of remedying the problem indicate the general awareness of the situation. The articles appeared in the Baltimore American, The Sun (Baltimore), The Press (Pittsburg).

124. Letter, W. K. Brooks to D. C. Gilman, 1878.

125. A complete list of Brooks's students is listed under "List of Dissertations, 1878-1919," Johns Hopkins University, Report of the President (1920), pp. 80-83.

126. E. G. Conklin, "Biographical Memoir of William Keith Brooks," p. 74.

127. J. Franklin Daniel was a Bruce Fellow at Johns Hopkins University. He did his work in physiology at the very end of Brooks's career. The Daniels moved to Berkeley after he finished his graduate work at Johns Hopkins. There he continued a successful career.

128. Letter, W. K. Brooks to D. C. Gilman, August 2, 1881, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

129. E. G. Conklin, "Biographical Memoir of William Keith Brooks," p. 77.

130. *Ibid.*, pp. 76-77.

Chapter Three: Brooks as a Nineteenth-Century Research Scientist

The scientific career of William Keith Brooks can be conveniently divided into two periods. The first part of his career began with his research conducted while he was working at the MCZ, primarily under the direction of Alexander Agassiz. This period, during which Brooks's research interests centered around the life histories and developmental stages of selected invertebrates, continued into the early or mid-1890's. It was during this time that Brooks spent virtually every summer at the various seaside locations of the CZL. It was also during this same time span that the vast majority of Brooks's scientific publications of a research nature were written. Indeed, the marine environment of the CZL provided Brooks with the primary subject for his publications.[1]

The second portion of Brooks's career as a nineteenth-century scientist can be dated from the mid-1890's until his death in 1908. This period was characterized by Brooks's interest in biological matters of a more theoretical, speculative and philosophical nature. While the roots of this interest clearly date to the beginning of his career, it was not until this latter period that Brooks appeared to concentrate upon these matters. The publications from about 1895-1908 were markedly different from those of the earlier period. No longer did Brooks publish primarily the results of his research; in fact, most articles from this latter period had a more general flavor to them and, as a result, were mainly published in periodicals with a much more general readership.[2]

In spite of the clear demarcation of Brooks's career into these two periods, there was a basic continuity throughout his work. Whether one examines Brooks's work in pure morphology or whether his more theoretical and philosophical works are consulted, he represented in both cases the epitome of a nineteenth-century biologist. His interests, his research questions, his method of inquiry, and his theoretical underpinings were all dependent upon and can be most clearly understood in light of his position in the nineteenth century. In this chapter, Brooks's research activities will be examined, both in terms of the work itself and in terms of the way the work fit into the late nineteenth century.[3] Brooks's research will be presented and discussed by biological group. His work of a more theoretical nature will be examined in a later chapter.

The early direction of Brooks's research was largely shaped by his exposure to E. S. Morse, Alpheus Hyatt and Alexander Agassiz. From the first two, he gained an appreciation for the role of scientific investigations upon molluscan development and its potential bearing upon the phyletic history of the whole group. From Agassiz, Brooks received much encouragement for pursuing embryological examinations of invertebrates and also received his initial exposure to the salps, a group he was to investigate throughout his lifetime.

1. Molluscan research

Brooks's earliest studies were on the molluscs, brachiopods and tunicates. In terms of the phylum Mollusca, Brooks's interest involved an attempt to uncover the clear relationship among the many diverse molluscan forms. His dissertation, which was published as "Embryology of the fresh water mussel,"[4] was aimed at demonstrating the shared developmental history of the freshwater lamellibranchs. The problem was that the embryos of Anodonta and Unio could be clearly distinguished as distinct forms. Brooks was able to demonstrate that at a very early embryonic stage the gastrulas and veligers of the two species exhibited marked similarities to each other. Later modifications resulted from the presence of dissimilar conditions acting upon each species during embryonic development. Brooks concluded that the descent of species could be determined through embryological examinations but that this method necessitated a complete history of several related species.[5] Only by using this approach was one able to separate shared characteristics of the group from acquired characteristics of the species.

This cautious attitude toward phylogenetic relationships and the need to support solidly any hypothetical ancestry became the characteristic feature of Brooks's morphological work. At this time, the work on molluscan relationships was quite confused and contradictory. Many connections between molluscan groups had been made that were erroneous.[6] In particular, it was widely held that the entire molluscan line was monophyletic, with the lamellibranchs serving as the primitive condition leading to the more advanced Gasteropoda, Pteropoda, Cephalopoda, Polyplacophora and Scaphopoda. The problem was that all these groups represented such diverse forms that it was difficult to discover any basis for common ancestry. Brooks's initial approach was to examine the supposed link from the lamellibranchs to the gasteropods. He was able to demonstrate that the gills, shell and digestive organ of the lamellibranch were all specialized forms of the embryonic type that had no relationship to the same structures in the adult gasteropod.[7] Therefore, the lamellibranchs did not belong on the main line of molluscan development, but were most probably a side branch from an earlier ancestral form.

The lamellibranch and gasteropod research was the result of careful investigations of the early embryonic stages of all of these forms. From these studies Brooks again stressed the need for careful attention to these primitive stages of development. And, in fact, all molluscs appeared to share a free-swimming ancestral form of which the veliger embryo was the remnant. Brooks claimed that a veliger-like proto-mollusc was supported by the fact that a veliger larvae appeared in all the widely diverse molluscan groups.[7]

By 1880, Brooks had pushed his embryological examinations back in development to include considerations of segmentation of the egg. By comparing various molluscan eggs in terms of their segmentation pattern, he was able to affirm his earlier position on the relationship of the lamellibranch group to the remainder of the molluscs. In a paper entitled "The acquisition and loss of food yolk in molluscan eggs,"[9] Brooks demonstrated that the lamellibranch (Ostrea virginiana, Chesapeake oyster) had a peculiar segmentation pattern in common with more primitive molluscs. These other molluscs laid large eggs, few in number with a large amount of yolk that determined the pattern of segmentation. The assumption by Ostrea of a sedentary mode of life demanded an increase in the number of eggs to insure reproductive success. To accomplish this, the egg size was reduced, the food yolk gradually lost but the segmentation pattern was retained.[10] This provided Brooks with additional evidence for the systematic position of the Lamellibranchiata as a specialized side branch of the molluscan line.

Brooks's used the same approach on the other molluscan groups. By looking at the segmentation patterns of certain prosobranchs, pulmonates, cephalopods and scaphopods, he noted that their early cell cleavages were remarkably similar. This he attributed to a closer affinity among these organisms than with the lamellibranchs. However, there were still many problems associated with the development of various molluscans beyond this shared segmental state.

> . . . and I do not think that any one who is acquainted with the recent literature on the development of Mollusca will dispute the statement that our knowledge of the mode of origin of the endoderm, the digestive cavity, the mouth and the anus in the various groups of the Molluscs is at present too fragmentary and inconsistent to admit of any special comparisons.[11]

The paper from which this quotation was selected included Brooks's detailed studies of the development of the endoderm, digestive cavity, mouth and anus in several pulmonates and lamellibranchs. His subsequent molluscan research was, in the main, an attempt to clear the inconsistencies relating to these developmental problems.

In "Observations upon the early stages in the development of the fresh-water pulmonates,"[12] Brooks stated that his intent was "to give purely descriptive information, which will serve as a basis for future discussion."[13] The need for this data was expecially acute since the two "most valuable and accurate papers" on the development of pulmonates were contradictory and left the whole question "in great obscurity."[14] The previous error of these papers, by E. Ray Lankester and Carl Rabl, had been compounded by the other important works available on pulmonates by M. Ganin (n.d.), Hermann von Jhering (1850-1930) and Hermann Fol.[15] To correct the inaccuracies, Brooks provided detailed investigations of the pulmonates _Physia_, _Limnaeus_ and _Planorbis_ with absolutely no theoretical or speculative comments. True to his intent to "contribute the beginning of a basis for the general discussion,"[16] he instead restricted the paper to his morphological investigations of the pulmonates. From the three species he observed, Brooks was able to provide a detailed description of the generalized development within Pulmonata. He began the work when the embryo divided into four cells. At this stage, Brooks was able to differentiate the embryo into primitive ectoderm and endoderm on the basis of the division of the four cells into micromeres and macromeres. The observations continued through the formation of a segmentation cavity, covering of the embryo by ectodermal cells, closing of the primitive blastopore, formation of the digestive cavity within the embryo, formation of the mouth as an independent invagination, migration of the anus from the original blastopore to a region near the mouth, opening of the digestive tract to the mouth and anus, and the formation of the shell area at the site of the primitive blastopore. Later developments, Brooks stated, were essentially as Lankester and Rabl had described. However, the previous works on pulmonates had been so inaccurate and contradictory, that the underlying uniformity of the early development had been obscured. Brooks hoped to remove this difficulty with his paper.[17]

In the same year the pulmonate paper was published, Brooks completed a paper on "The development of the squid."[18] The paper was the result of research Brooks conducted on the embryo of Loligo pealii during the summer of 1879 in Crisfield, Maryland. Again, it was his interest in the paper to contribute the necessary information to the embryonic development of the group in order that the systematic position of the Cephalopoda would be clarified. Until his work, knowledge of the cephalopods was limited to the work of A. Kölliker (1870-1905) on the embryo of Sepia officinalis and H. Grenacher's (1843-1923) studies on an unknown decapod cephalopod.[19] The problem Brooks faced was twofold. First, the existing literature was quite sketchy and did not offer a complete embryonic history. Second, the three observations tended to illustrate the marked embryonic differences between Loligo, Sepia and Grenacher's embryo (as it was referred to). This second problem was due to the long and complicated phylogenetic history of the cephalopods, the most highly developed invertebrate. In this long history, much of the embryonic record had become simplified so the ontogeny of the group appeared unclear.[20] The solution to both problems was attention to the details of early embryonic history. At these stages the primitive shell area, mantle primordia and the form and position of the early gill structures were very uniform. Brooks was able to demonstrate clearly that these early features of the squid embryo illustrated its relationship to the typical mollusc. Brooks stated that subsequent specializations in the cephalopod branch had made the exact origin and development of the squid unclear. But the mollusc link was evident. It was crucial, as a result, to examine the early ontogenetic record.

> The only basis for an homology of the Mollusca, in the absence of a phylogenetic record, and of transitional forms, is therefore to be sought in the comparison of early stages in the development of individuals of the different groups, at a time when the specializations of structure, characteristic of the adult forms, have not yet made their appearance.[21]

It was for this reason that Brooks rejected the speculations of other morphologists who attempted to find homological relations between the siphons and arms of cephalopods and structures in related molluscs. The embryonic record presented clear evidence that these appendages were later modifications.[22] In order to theorize about shared ancestry, therefore, Brooks insisted that solid embryological support buttressed the claim.

Although much of Brooks's work on Mollusca was prompted by his desire to either correct or add to the information concerning the group's systematic position, some of it did have a practical application. For example, in Brooks's letter to D. C. Gilman proposing that Johns Hopkins develop a seaside laboratory, Brooks stated that one of his desires was to study the Chesapeake oyster, from both a developmental and a practical standpoint.[23] Brooks's intention was to obtain more information concerning the oyster in order to be of possible aid to the oyster industry.

The oyster work began at Fort Wool in 1878. Brooks had consulted the literature concerning the breeding habits of the oyster. All the published papers available stated that fertilization and early development took place inside the parental shell.[24] Following the procedure published in the papers Brooks

> . . . opened numbers of oysters during the summer of 1878, and carefully examined the contents of the gills and mantle chambers, but found no young oysters. I concluded that the time during which the young are carried by the parent must be so short that I had missed it, and I entered upon the work this season [1879] with the determination to examine adult oysters every day, through the breeding season, in search of young, and at the same time to try to raise the young for myself by artificially fertilizing the eggs after I had removed them from the body of the parent.[25]

The summer of 1879 was more successful than the summer of 1878. Within forty-eight hours after setting up the CZL at Crisfield, Brooks found three females and one male with ripe gametes.

> I mixed the contents of the reproductive organs of these four oysters, and within two hours after the commencement of my first experiment, I learned by the microscope that the attempt at artificial fertilization was successful, and that nearly all of my eggs had started on their long path toward the adult form.[26]

More work during that summer provided Brooks with the evidence to conclude that *Ostrea virginiana* was reproductively unisexual, that the eggs were fertilized externally and that the development of the oyster paralleled that of the development observed in the lamellibranch group.[27]

The practical nature of the work was contained in Brooks's report he submitted to the Maryland Commission of Fisheries in 1880, "The development of the American oyster."[28] Brooks wrote the report in two sections. The first was intended as a popular description of the oyster, its method of propagation and the possibility of artificial fertilization of the oyster. The second part contained the scientific description, complete with microscopical sections, of the development of Ostrea. The work was of such notable quality and had such scientific and practical merit that Brooks was awarded the medal of the Société d'Acclimatation of Paris in 1881.[29]

Implicit in Brooks's report was a warning that over harvesting the native oyster could lead to exhaustion of the resource. One possible solution was to raise artificially oysters to replace those that were harvested. The problem confronting this solution was that Brooks had only been successful in rearing the oysters through the early embryonic stages. After this period the mortality rate was so high that in eight days all the embryos were dead. In the summer of 1882, Brooks found that by supplying the water with lime through the use of macerated oyster shells (calcium carbonate source), the embryos not only survived longer, but grew at a much more rapid rate.[30] By 1883, Brooks and J. A. Ryder (1852-1895) had constructed an oyster culture apparatus that allowed them to change the water without losing embryos. This had been the greatest problem to overcome in the artificial propagation experiments.[31] Brooks and several graduate students continued the oyster work until 1885 when Brooks was able to report to Gilman that it was possible to rear oysters in the laboratory and then to transfer them to floating "beds" for the remainder of their development.[32]

The report of 1880 also served to establish Brooks as one of the major authorities on oyster development. As a result, he was appointed by the state legislature as Chairman of the Oyster Commission in 1882. The commission was established to investigate the oyster industry in terms of alleged over-dredging, inadequate supervision and danger of depletion.[33] Until 1884 the commission inspected oyster sites, sampled and measured oysters, examined fishing records and interviewed oyster industry officials. The conclusion was that the oyster population was diminishing as a result of a greater demand upon the oyster stock that its replacement rate.[34] The recommendation by the commission was that a comprehensive system of oyster farms utilizing propagation should be implemented that would supplement the natural reproductive abilities of the oyster. In addition, much stronger enforcement of laws was advocated, the periodic closure of breeding areas was encouraged and a permanent oyster regulatory agency was suggested.[35] Unfortunately, private enterprise was successful in blocking the intervention of any governmental regulatory body. The bill Brooks's commission presented to the Maryland Assembly at the end of the report of 1884 was shelved. Brooks continued to press for conservation measures and for regulation of the oyster industry as the production of native oysters continued to fall.[36] In 1891, The

Oyster, A Popular Summary of a Scientific Study was published by Johns Hopkins to popularize the story of the oyster and to increase the public's awareness of the problem in an attempt to create publicity for change.[37] President Gilman wrote the introduction to the work.

> To show what is possible for the propagation and protection of young oysters, he [Brooks] describes in the most interesting manner, in terms scientific enough to be accurate, not so scientific as to be hard of understanding, the life-history of the bivalve. The oyster's exposure to infantile dangers, its preferred home, its dietary habits, its susceptibility of culture, its wonderful fecundity, are vividly portrayed. Indeed, this modest volume is at once a memoir in natural history and a chapter of political economy.[38]

It was not until one year after the second edition of The Oyster that any change was enacted.[39] In 1906, the Maryland Assembly passed a bill that placed into effect virtually all of the recommendations that the Oyster Commission had made in 1884.

2. Brachiopod research

Brooks's involvement on the Oyster Commission effectively ended his personal research into developmental questions concerning other molluscs. In addition, after his tenure on the commission, Brooks did very little original research on the oyster, leaving most of the work to his graduate students. The only exception to this generalization was his preparation for the publication of The Oyster in 1891 and its republication, as a second edition, in 1906. A similar pattern was seen in Brooks's studies of the phylum Brachiopoda.

The brachiopods were among the several unusual groups of organisms that were variously classified by the systematic morphologists in the late nineteenth century. Prior to descent theory, the brachiopods had been included under the vermian stem. However, work in the latter part of the century broke this group into its "natural" categories. The result was to treat brachiopods as a separate group or to consider them as closely related to Polyzoa or to consider the Brachiopoda as a member of the lophophore group, Molluscoida, along with the bryozoans and phoronids. Brachiopods were also of interest because of the apparent segmental embryonic forms which could have a bearing upon its ancestry.

Brooks's interest in the brachiopod group stemmed from his days at the MCZ. While he was working on the embryology of the freshwater mussels, he noticed similarities between the molluscs and the brachiopods. By examining several brachiopods he

> . . . reached results of considerable interest; showing, among other things, that the worm-like features of Brachiopoda do not justify their removal from among the Mollusca, as unquestionable Molluscs have nearly as well marked worm-like characteristics in the earlier stages of their development.[40]

Moreover, the close affinity between the veliger of the molluscs and the lophophore-bearing polyzoan larvae, led Brooks to consider the molluscs and Molluscoida as closely related.

> . . . and it becomes plain, not only that the Molluscs and Molluscoida are related, but that they are connected so closely, that the advisability of such a division is very doubtful. We also obtain, at the same time, an explanation of the worm-like early stages of the embryo, exhibited by so many of the true Mollusca.[41]

Brooks suggested that the connection was from a common stock. The ancestor was most likely vermian in appearance. From this group, the brachiopods, polyzoans and the veliger stem to the Mollusca branched off.[42]

The probable phylogeny Brooks offered for the brachiopods and molluscs was not tendered without knowledge of its tenuous state. Brooks realized that the lack of clear brachiopod life histories made such an effort less than well-founded.

> The imperfection of our present knowledge cannot, however, be fairly urged to restrain us from making as much use as possible of what knowledge we do possess, although we must constantly bear in mind that it introduces an element of uncertainty into all our conclusions. This, of course, is true of all biological speculation at present, but no one would advocate the abandonment of all speculation and comparison until all the facts of our science have been recorded and verified.[43]

To alleviate the speculative problem, Brooks set out to investigate the life history of some representative brachiopods. In the summer of 1878, he found Lingula pyramidata, a hingeless brachiopod (Inarticulata), in its embryonic form. Since Lingula had not been examined in this form and "nothing was known of its development," part of the summer was spent in tracing the life history from a very early embryonic stage to the adult form.[44] The results were published later in the same year.[45]

Brooks's paper began with a discussion of the current literature on brachiopods in which the works of Huxley, Claus, Gegenbaur, Lankester, Morse and Packard were all shown to be in disagreement. The confusion was due to the ancient history of the group that allowed the members to undergo a marked amount of embryonic specialization. Since only a few isolated species were available to these naturalists, there appeared to be little coherence in the group. More recent work by Felix Lacaze-Duthiers (1821-1901), Morse and Kowalewsky provided fairly complete and coherent information concerning the embryology of both hinged and hingeless forms. The result was that all the embryos could be represented by an ideal archetypic embryo which Brooks viewed as the ancestor of most invertebrates. Lankester's "telostomiate architrochic" larva represented the stem form. Furthermore, these embryos were extremely similar to the embryo of Loxosoma, a polyzoa. Brooks concluded that the brachiopod and polyzoa line likely were modified from the same stock, the architrochic embryo.[46] To complete the phylogeny, it was from the same stock that the proto-mollusc was derived. The veliger embryo of molluscs and the trochifera embryo of the polyzoans and brachiopods shared the same stem. By studying the life history of Lingula Brooks was able to provide additional information to his speculative views in "On the affinity of the Mollusca and Molluscoida." Instead of referring to the ancestor as "vermian stock" Brooks was able to identify it as a trochifera due to the presence of a conspicuous trochal disc. From this form the brachiopods developed through a polyzoa-like ancestor, while the veliger form of the mollusc developed directly from the trochifer.

The 1878 paper on brachiopods represented Brooks's final research on the group although several students worked on various developmental questions of Lingula at later CZL sessions. The research, while short-lived, did aid in establishing Brooks's international reputation. An abstract of the Lingula work was published in Paris in 1881, the same year Brooks won the medal for his oyster work from the Société d'Acclimatation.[47] Brooks also wrote to D. C. Gilman that several European "naturalists" had expressed an interest in the Lingula work and had written Brooks favorable letters concerning the work.[48]

3. Tunicate research

Although Brooks's mollusc and brachiopod research was largely confined to the first ten years of his career, he maintained a life-long research program on the tunicates. The work dated from the research Brooks had conducted at the Newport laboratory on the tunicate genus Salpa.[49] Alexander Agassiz had suggested to Brooks that the salps would be interesting to work on because of their supposed intermediate position between Amphioxus and the vertebrate line. Because there was much uncertainty concerning this link and much interest in problems of vertebrate ancestry from an archtypal proto-chordate, any information the salps would have on these questions would be enthusiastically received by the morphological community.[50] Additionally, Salpa was an ideal specimen to study. Off the coast of Newport, it occurred in abundance, often clogging plankton nets that were being used to gether other pelagic forms. And, Salpa had a transparent tunic. This characteristic enabled the investigator to observe the anatomy of the living form without the need of dissection.

The results of Brooks's study of Salpa during the summer of 1875 were published in a brief form in three articles in 1875 and 1876.[51] In his typical style, Brooks stated that his work was aimed in the direction of correcting previous errors by other naturalists. Noting that tunicates had been formerly classed with the molluscs due to superficial resemblances, Brooks also observed that much of the work done to link tunicates with vertebrates had included erroneous observations. Salpa is an unusual organism in that it exists as both a solitary form and in colonies or chains. In 1814 Chamisso (1781-1838) had noted this fact and had referred to it as an example of "alternation of generation."[52] Subsequent work by Huxley, Michael Sars (1806-1869), A. Krohn (184?-1891), Karl Vogt (1817-1895) and Karl Leuckart (1822-1898) had agreed with the alternation of generation hypothesis. They observed that the salp embryo became a solitary, sexless adult salp. This form produced, by budding, a chain of salps containing eggs and furnished with testicular tissue. Upon maturation, the testis produced sperm which fertilized the egg to produce more solitary, sexless salps. Since the life history alternated between an asexual stage (solitary) and a sexual stage (chain), it was thought that the organism exhibited true alternation of generation. Such an observation was remarkable because this would mean that the tunicates exhibited characteristics normally observed only in phyla of a lower taxonomic standing. Any attempt to link these organisms to the Chordata line would necessarily involve an explanation for the occurrence of such a primitive life history in an advanced form.

Brooks's work, on the other hand, demonstrated that the previous studies on Salpa were in error. By examining the early development of the solitary and chain forms, Brooks observed a different situation. The solitary salp produced the chain by budding from the muscular tunic of its body wall. The chain originated as a tube or stolon. As the stolon developed, Brooks noticed that eggs were transported to the tube. These eggs were produced from ovarian tissue in the solitary form. As the stolon elongated, more eggs were deposited until the chain became lined on both sides with eggs. As the chain matured, placenta-like supporting tissue surrounded each egg and nourished it in its development. Once the egg was mature, it was discharged. Then, the tissue of the chain form became sexually mature as testes, discharging spermatic fluid that would fertilize eggs produced from another solitary salp. Brooks concluded, therefore, that the solitary salp was a female. It produced both the male stage by budding and produced eggs from ovarian tissue. The chain salp served as a nurse for the eggs and for the production of sperm.[53] Salpa, then, did not exhibit alternation of generation but merely an unusual separation of the sexes.[54]

The brief papers were followed by an extensive publication, "The development of Salpa," published late in 1876.[55] In this work, Brooks again cited all the previous works on Salpa and noted that his own observations did not differ substantially from most of the information in those papers. However, none of the other works (Huxley, Sars, Krohn, Vogt and Leuckart) had described the reproductive organs of the salp, except for a brief examination by Leuckart.[56] Therefore Leuckart's views, which were incorrect, prevailed.

> It is now a settled fact that the reproductive organs are found only in the aggregated individuals of Salpa, while the solitary individuals, which are produced from the fertilized eggs have, in place of sexual organs, a bud-stolon, and reproduce in the asexual manner exclusively, by the formation of buds. Male and female organs are, so far as we yet know, united in the Salpae in one individual. The Salpae are hermaphroditic.[57]

Brooks stated, in correction of Leuckart, that upon inspection of the egg in the chain salp that it had a mature appearance at all stages of chain growth, even when the chain consisted mainly of undifferentiated cells. He concluded that the chain could not be the parent of an already fully formed egg. Obviously, the eggs were formed previously in the ovarian tissue of the solitary salp.[58] Brooks's summary of salp development followed the same outline of his previous works.

The paper went on to discuss the importance of the separation of sexes seen in *Salpa*. Brooks noted that the dependence of the male upon the female was also seen in other groups, Arthropoda (bees and barnacles especially) providing several examples. Additionally, many tunicates exhibited similar sexual separation (*Pyrosoma*, *Didemmium*, *Perophora*, *Annauricium* and *Botryllus*).[59] All of these examples illustrated the common factor that dissimilar sexual stages or non-synchronized maturation insured that the species would not be self-fertilized. *Salpa*, Brooks maintained, represented another case of this adaptation.

Brooks continued with the paper to detail the contribution his work had upon the phylogeny of the salps and upon the possible origin of the separate sexual stages. However, he explicitly noted that in this venture he was departing from a strict scientific method.

> As the remainder of this paper will be mainly theoretical and speculative, I must state here that while I fully realize the difference between observations as to the way in which a phenomenon has been, and speculations as to the way in which it may have been brought about, it does not seem best to omit all theoretical discussion, although the views here advanced may be very much modified or entirely replaced by subsequent discoveries.[60]

Brooks, therefore, realized that the observational aspects of his work were based upon a more firm basis than were the speculative aspects. Nevertheless, such information had a value, if it was only to encourage additional research.

Brooks's research activities on the oyster created a six-year hiatus in his salp work. He returned to the study in 1882 to respond to a series of articles by Wladimir Salensky (1847-1918) that were critical of the research of Brooks and Kowalewsky that demonstrated the existence of ovaries in the solitary salp.[61] Salensky claimed that the eggs of salp could be traced back to undifferentiated embryonic cells at the base of the budding stolon. These cells then gave rise to ovaries in the salp chain. Salensky stated, therefore, that the solitary salp was sexless, the chain salp was hermaphroditic and the species exhibited alternation of generation.

The work Brooks conducted to answer Salensky's critique is of interest because it marks the full-scale application of new histological and microscopical techniques to embryological and developmental work. The previous work on Salpa had been done largely upon whole specimens. This was not a bad procedure since the salps have a clear tunic that enabled one to examine closely the internal structure. However, for questions of fine resolution, such as differentiating between ovarian tissue and undifferentiated tissue, careful microscope work was needed. Obtaining his salps from Spencer F. Baird (1823-1886) and A. E. Verrill, Brooks had "several thousand sections" made of the solitary salp by the Baltimore physician Dr. I. Bermann.[62] In preparing the sections Brooks also learned from Bermann the latest techniques for staining, imbedding, cutting and mounting the sections. The more precise sectioning practices enabled Brooks to make extremely careful observations upon hundreds of sections, including both transverse and longitudinal sections.

Brooks's accounts of his work were published in 1882 as "Chamisso and the discovery of alternation of generation"[63] and as "The origin of the eggs of Salpa."[64] Both works contained much microscopical detail concerning the examination of the solitary salp. Such detail, especially by providing longitudinal sections to complement Salensky's transverse section work, allowed Brooks to verify many of Salensky's observations and, more importantly, to correct the erroneous views.

> . . . careful examination of very thin sections of my perfectly preserved specimens show that the minute details of his [Salensky] account are far from correct, probably because his specimens were not perfectly perserved, or perhaps they were not sufficiently hardened to furnish very thin sections.[65]

Among the corrections, Brooks demonstrated that the digestive cavity of the salp chain formed just as it did in other tunicates, and not from endoderm as Salensky believed.[66] Furthermore, by examining under high magnification the tissue Salensky claimed was endoderm, Brooks showed that the granular ground substance actually contained germinal cells.

> When a very thin section is examined with a high power, Figure 5, each of the oval transparent bodies is seen to be a germinative vesicle, with a nucleolus suspended in its cavity by a protoplasmic reticulum of fine branching threads; and surrounded by a granular layer of yolk which is rendered angular and polygonal by the pressure of adjacent eggs. I have obtained a complete series of sections showing the eggs at every stage, from the one just described, up to the time when the single eggs are attached, by their gubernacula, to the wall of the branchial sac of the chain Salpa, and no one who examines the series, can doubt for an instant that the bodies in Figure 1, not only develop into eggs, but that they are actually eggs, differing very slightly from the mature egg.[67]

Therefore, the "endoderm" did not change character, but was actually made of true eggs. The solitary salp, as a result, was still a female and alternation of generation was not a characteristic of Salpa.

The salp work reached its apex in 1893 with the publication of The Genus Salpa.[68] According to Brooks, the monograph represented the culmination of research on the salps that he began shortly after he published the preliminary papers on the species in 1875 and 1876.[69] He had originally planned to complete the work for publication in 1887, but due to the need for microscopical sections and the need of a financial appropriation from the trustees of Johns Hopkins to cover printing costs, the project was delayed until 1893.[70] Regardless of the delay, the work was an impressive production.[71] The review published in Popular Science Monthly referred to The Genus Salpa as a "monumental work" and a "credit to American science."[72]

Despite the favorable reaction to the work, The Genus Salpa did not offer much in the way of new information to the series of scientific publications Brooks had previously written. However, for the first time all this information was presented in one work. The first portion of the monograph, "A general account of the life history of Salpa," provided a complete bibliography of all the important scientific literature on Salpa, including several of Brooks's previous papers. Each work was evaluated critically in light of Brooks's research. The section concluded with a detailed account of the life history of Salpa. The second part, "The systematic affinity of Salpa and its relation to the conditions of primitive pelagic life; the phylogeny of the Tunicate; and the ancestry of the Chordata," represented the speculative phylogenetic considerations of the group.[73] In the typical style of Brooks, these hypothetical views were not offered until the species had been examined by extensive observations (Part 1). And, Brooks emphasized that such speculations were of a much more tenuous nature than facts from observations. In spite of the lack of certainty, there was the need and value to the speculative work.

> We must remember, though, that it is possible to make instructive and valuable comparisons even when they do not lead to exact or definite phylogenetic conclusions, as when we compare adult echinoderms with each other without committing ourselves to any view of their ancestral relationship; and I think we may give clearness and definiteness to our conception of the salpa embryo by comparing it with the embryo of other Tunicates, although we may not be able to mark out the path it has followed in reaching its present structure. We cannot have a clear notion of structure without historical data.[74]

The book concluded with a section, "A critical discussion of my own observations and those of other writers, on the sexual and asexual development of Salpa." In this section, Brooks again examined the work of other morphologists concerning the supposed sexual and asexual stages of _Salpa_. Basing his own views on the microscopical data, he demonstrated that the dimorphism exhibited by _Salpa_ represented different sexes. Moreover, the pattern of sexual separation of the species was not peculiar, but could be explained on the basis of phylogenetic considerations.

> The solitary salpa produces ovarian eggs, and, like its ancestors and like pyrosoma, passes them into buds to mature and ripen and develop. As the aggregated salpae do not bud, they have lost their ancestral ovaries, and all the female germ cells now remain in the body of the solitary salpa at the base of the stolon and form its ovary, _as they formed the ovary of the primitive tunicate from which the method of budding has been inherited_. The testis of the solitary salpa remains embryonic, its cells multiply by karyokinesis and grow into the stolon, and give rise to the testes of the chain-salpae, which, however contains no female germ cells and produce no eggs.[75]

In addition to providing a comprehensive examination of the genus _Salpa_, Brooks's monograph served to represent an example of morphological research _par excellence_. The descriptions of the life history of the species and examinations of the body structure were given with extreme attention to detail. Crucial body structures were examined utilizing longitudinal, horizontal and transverse sections to obtain the most accurate details possible. Brooks also consulted several anatomists in the Baltimore region concerning the best sectioning techniques.[76] The result of the attention given to microscopical detail was the presentation of forty-six plates with numberous figures to supplement the text.[77]

Brooks continued to publish papers on the tunicates throughout the 1890's. Most of these were extracts from The Genus Salpa, although he did publish one paper, "The nutrition of the Salpa embryo," to clarify the lack of homological relationship between the mammalian placenta and the salp "placenta" or nutritive structure.[78] Two other works, published in the early twentieth century, concerned relationships of several new species of tunicates. In a purely descriptive paper, "The affinities of the pelagic tunicates. No. 1. On a new Pyrosoma," Brooks described the species in detail, suggesting its possible relation to other tunicates.[79] Brooks's final published paper of his life, printed shortly after his death in 1908, included descriptive work on the tunicates he had investigated since the publication of The Genus Salpa. The paper, "The pelagic tunicata of the Gulf Stream," included descriptions of *Salpa floridana*, the subgenus *Cyclosalpa* and the appendicularian *Oikopleura tortugensis*.[80] The last species represented an interest Brooks developed in 1894 at Beaufort.

> Appendicularia is the modern representative of the tailed larva of Tunicates, and the oldest representative of the Vertebrate line, and its life history must be very instructive, but no one has found the eggs or young although the animal is found in all

> seas. We have found out the difficulty, and hope to get its life history.[81]

From 1894 until his death, Brooks continued the work on appendicularians with the goal of providing the necessary details of its life history to allow an accurate comparison with other tunicates.

Brooks's entire research program on the genus Salpa and related urochordates originally stemmed from his interest in correcting the alleged alternation of generation of the group. His original observations were primarily macroscopic in nature. In the 1880's, as microscopical and histological techniques became refined and applied to developmental studies, Brooks utilized these methods. This enabled him to make the necessary examination of cell layers and tissues to determine that the solitary salp did produce eggs and that the salp-chain only contained testicular tissue. Of subsequent interest were questions surrounding the systematic position of the tunicates.[82] These problems were also largely dependent upon the observational work Brooks had conducted upon the species.

4. Arthropoda research

The same attention to detail Brooks exhibited in his salp work was also characteristic of his work on the arthropod class, Crustacea. The crustacean research was mainly confined to the years 1878-1886. Despite the brevity of Brooks's attention to these organisms, this research was among the most impressive Brooks conducted and, in many ways, may have been the most influential.[83] These studies did not, like the tunicate and mollusc work, utilize as much microscopical work for most of the examinations were upon diversified larval types which were of considerable size. As a result, the character of this work was of attention to detailed body structure and not to cell or tissue layers.

Like so much of Brooks's work, his interest in Crustacea was initiated by the discovery of a larval form during one of the early summer sessions of the CZL. In 1878, Brooks studied one of the only common stomatopod crustaceans on the Atlantic coast, Squilla empusa, which he found to be very common in the Chesapeake.[84] Squilla was of tremendous morphological interest because it represented the simplest expression of the highly complicated larval metamorphosis of higher Crustacea. In particular, the zoea larval stage of Squilla bore a more intimate relation to the adult form than exhibited in the other stalk-eyed Crustacea.[85] The main issue was that in the only reports available on squilloid development, the larval history was confused. Fritz Müller had published an account that stated the species passed through two larval stages, Erichthoidina and Alima, while C. Claus stated that development was only through an Alima larva.[86]

In addressing the Squilla problem, Brooks recognized that the confusion was due to the fact that stomatopods exhibited many larval types. In fact, the group was an exception to the general morphological rule that the larval stages are less diverse than the adult. Brooks further felt that more work would demonstrate additional larval forms to the Erichthoidina and Alima.

> From some unpublished observation by Faxon, which I have had the opportunity to examine, I am led to believe that these two forms of development are not the only ones which will be found to occur among the Stomatopods, and that this very complicated department of embryology demands careful observation of the actual metamorphosis of the larva, in as many species as possible, a work which can be carried on no where but at a sea-side laboratory.[87]

Although Brooks was not successful in obtaining eggs of Squilla and observing the development from this early stage, he did obtain a wide-range distribution of larval stages and followed their development.[88] By careful attention to and descriptions of the carapace development, segment details, appendage structure and the telson, Brooks was able to describe completely the larval life history of Squilla empusa. The work confirmed Claus's view that squilloid development only involved metamorphosis through the Alima larval stage.[89]

During the summer of 1880, Brooks worked upon the life history of another crustacean, the decapod Lucifer acestra.[90] He viewed the work as very important for morphology since ". . . the development of Leucifer [sic] is one of the most interesting life histories which has been studied."[91] In detailing the importance of the research to President Gilman, he wrote the following.

> I suppose you know that, while the ontogeny of the individual tends to recapitulate the phylogeny of the group, yet the life history of most of the higher animals has been so much modified that most of the stages which would indicate the phylogeny, are lost, or left out of the embryonic history. Once in a while, though, an animal is found, which has retained the ancestral manner of development, without modification, and these forms are of the greatest scientific interest; for one life history of this kind contributes more to the science of morphology than any number of modified life-histories. There is no way of telling whether a given animal will be found, when it is studied, to have an ancestral, or a modified manner of

> development, but occasionally some observer has the good fortune to find a form of development, which is of the unmodified kind, and which puts the facts which have been observed upon allied forms in their true light.
>
> Leucifer happens to be an animal of this kind. Its life history is perfectly unmodified, or ancestral, and stages which have been dropped from the history of all other Crustacea are preserved by the Leucifer embryo with beautiful definitions and simplicity.
>
> In the flood of light which it throws on the history of the Crustacea in general the Leucifer embryology is like the discovery of a key to an unknown litterature [sic].
>
> One of the interesting points is the presence of a Nauplius stage. The lower Crustacea generally pass through a Nauplius stage, while the higher Crustacea do not. As the remote ancestors of all the Crustacea must have been the same, we must conclude that the high forms once passed through a Nauplius stage, but have lost it. Several years ago, Fritz Müller stated that one species of Prawn [sic] leaves the egg as a Nauplius, but the development of other prawns has since been studied and as none of them have such a stage, there has been some doubt whether Müller did not make a mistake.
>
> He did not raise his embryos, but caught them in the ocean, and Mr. Agassiz has always held that he had got hold of some other embryo. I have seen Leucifer lay its eggs, and I have seen the Nauplius hatch from the egg, so the occurrence of a Nauplius stage in one Decapod Crustacean is absolutely proved.[92]

The fact that Lucifer had a nauplius stage in its larval history was viewed by Brooks as the piece of evidence that linked the low and high Crustacea through the same remote ancestor. The results of this work were immediately published in both the United States, "The young of the crustacean Lucifer, a nauplius,"[93] and in Europe, "The embryology and metamorphosis of the Sergestidae."[94] Both articles stressed the correction of Müller's work by Brooks's observation of the nauplius stage in Lucifer.

Brooks also wrote to Walter Faxon at Harvard concerning the importance of the Lucifer work. Stating that the existence of a nauplius stage in this group was significant for the systematic position of the decapods, Brooks downplayed the hypothesis of crustacean phylogeny that included a metameric form.

> The various Decapods are not the descendants of an ancestral crustacean, with twenty similar unspecialized somites, but of an ancestral form with a small number of specialized somites.[95]

The same theme was echoed in a letter to T. H. Huxley:

> . . . show that the life history of the Sergestidae [section Penacidea of the order Decapoda] is the most significant Crustacean embryology which has since been worked out . . . . the Crustacea are descendants of a Nauplius-like ancestor, with only three pairs of highly specialized appendages, instead of a great number of pairs of unspecialized appendages . . .[96]

Brooks's letter to Huxley contained not only the results of the *Lucifer* work, but also a plea for Huxley to aid Brooks in having the *Lucifer* results published in Europe.[97] Huxley communicated Brooks's request to the Royal Society and the paper was published in the *Proceedings* in 1881[98] in an abstract form and in the *Philosophical Transactions* in 1882 in full form.[99]

The major publications on *Lucifer* provide another example of the meticulous approach Brooks took to research problems. The paper included a full literature review of the material available on *Lucifer*. While there were several studies on the adult stage, very little information was available on the important larval stages.[100] Much of the difficulty in observing the development was due to the difficulty in raising adults from eggs in captivity and from handling the fragile eggs for observation. These were not the only problems, however.

> When we add to this that the eggs are laid about 9 o'clock in the evening, and must be studied between this time and daylight, after several hours of laborious collecting, by eyes that have been already severely taxed with looking over the collections

> and picking out the transparent and almost invisible adults by an artificial light, and examining each one of them with a lens to find those which carry eggs, the difficulty of the subject will be appreciated.[101]

Despite the problems, Brooks was successful in observing the complete life history.

> As the result of my four months' efforts I can now state that I have seen the eggs of Lucifer pass out of the oviduct. I have seen the Nauplius embryo escape from the same egg which I had seen laid, and I have traced every moult from the Nauplius to the adult in isolated specimens. There is therefore no Crustacean with the metamorphosis of which we are more thoroughly acquainted than we now are with that of this extremely interesting genus.[102]

Brooks observed the metamorphosis of Lucifer in impressive detail. The development was traced molt-by-molt, beginning with the segmenting egg and moving through the larval stages of nauplius, protozoea, schizopod, immature Lucifer and, eventually to the adult form. This was followed by an examination of the history of each individual appendage through all of the molt stages.[103] All of this detail was necessary for each metamorphic stage had some significance for studies of the development of the higher Crustacea. For example, the protozoea stage was used by Claus to argue that the higher crustacean zoea larvae was a secondary modification of the protozoea; on the other hand, Dohrn and Müller argued that the protozea showed clearly the recapitulation in the zoea of an ancestral form.[104] However, Brooks felt that much more work of this same nature was required before any definitive view could be accepted.

> I am therefore unable to give CLAUS'S interpretation of the significance of these larvae unqualified acceptance at present, and feel that our groundwork in this department of knowledge

> can be made sure only by new observations. Every naturalist who can trace the whole life-history of a single species of any of the general of lower Malacostraca by actual moults, will not only help us to a sound and thorough appreciation of the significance of Crustacean embryology, but will also contribute to a better knowledge of the relation between ontogeny and phylogeny in the whole province of biology.[105]

In addition to the detail Brooks's study added to Lucifer development, the paper was important in stressing the appearance of the nauplius larvae.

After completion of the Lucifer work, Brooks returned to investigations upon Stomatopoda. Perhaps due to the publication in Philosophical Transactions, Brooks was asked to analyze the Stomatopoda from the Challenger expedition and to write the report on the group for the Challenger Report.[106] Brooks received the material, primarily larval stages, in 1883 and spent the next three years examining it. The result of the work was the publication of the "Report on the Stomatopoda collected by HMS Challenger during the years 1873-1876" in 1886.[107]

The Challenger work was essentially an extension of the Squilla project Brooks had published earlier. Consequently, he was faced with the same problems in studying these larval forms he had confronted before.

> As no one has succeeded in rearing them from the egg, and as they do not thrive in confinement, the only way to trace the life history of the Stomatopoda is by the comparison of the series of larvae which are collected in mid-ocean, and this is attended with peculiar difficulties, for the larval forms which have been described are more numerous than the known species of adults, and many of them unquestionably beong to species the adult stages of which have never been discovered.[108]

In addition, what aids that were available were not adequate in providing the necessary information.

> . . . as I soon found that the characteristics which have been selected for diagnosis are by no means the ones which are most significant and of most scientific importance. In most of the published descriptions little attention is given to points which are not regarded as diagnostic, and while most of the general are natural ones the points which are of greatest value in tracing the relation between the larvae and the adult are entirely ignored in most of the published descriptions.[109]

The method Brooks used to surmount these problems involved three approaches. First, each larval type or genus was identified by selecting or comparing larvae which were sufficiently alike to indicate they belonged to the same series. This method provided diagnostic relations and descriptions for an Alima larva, an Erichthina larva and an Erichthoidina larva. The second stage was to measure the larvae in each series (in thousandths of an inch). The result was that each series yielded decisive evidence of a molt relation. That is, each molt stage represented a discrete size increase over its preceding stage.[110] In this manner, Brooks was able to extract the species from the series. The final step in the identification process involved the reference of the larval type to the adult genus. The end result was that Brooks was able to provide coherence to a vast number of larval forms that were often erroneously labeled as distinct genera. It also provided many adult forms with their appropriate larval stages.

To complete the Stomatopoda analysis, Brooks then developed a diagnostic key that would unify the key features of the larval forms and the main adult features. An example of this work that joined the larval form Alima and the Squilla genus follows.

> Although Claus decided that they are young Lysiosquillae they show their relationship to the genus Squilla as distinguished from Lysiosquillae by the following characteristics, all of which are shared by all fully-grown Alima larvae. The dactylus of the raptorial claw has on its inner edge a small number of marginal spines, usually about five or siz; the hind body is wide and flat, and the postero-lateral angles of the abdominal somites end in acute spines. The outer edge of the proximal joint of the uropod is bordered by a small number of spines usually less than eight, and the inner one of the two spines on the ventral process from the posterior edge of the basal joint of the uropod is longer than the outer, and it has a tooth or lobe on its outer edge; and the telson has six marginal spines with minute secondary spines between the submedians, and four or more large secondary spines between the submedian and the second or intermediate, and usually a single one internal to the base of the third or lateral marginal spine. While it is true that all of these characteristics are not exhibited by every adult Squilla, there are no Stomatopods except those of this genus in which they are all united, and they are all of them present in most Squilla and in all the Alimae.[111]

The same type of notable attention to detail was presented by Brooks in his description of the stomatopod genera and species. Generic considerations included a general diagnosis of the group, remarks upon the key characteristics and ontogenetic details. For the species, the diagnosis of the group was followed by a general description, emphasizing precise measurements of all body parameters, habitat preferences of the species and general remarks on the species.[112] By providing such a detailed appraisal of the Stomatopoda, Brooks was successful in describing the Challenger samples. The end result was to organize many larval forms, which had been previously assigned the status of a separate genus, under their appropriate genera and to provide, in many cases, complete life-histories of forms that were known only in their adult stage.

Although Brooks's major contributions to the understanding of the development of Crustacea was primarily restricted to the stomatopods (Squilla) and the natantian decapods (Lucifer) he also contributed importantly in several other areas of crustacean work. First of all, Brooks's publications of his research on Arthropoda in both the United States and Europe included an encouragement for other workers to examine the group. Brooks believed that Crustacea was a particularly important group to study because of the number of transitional larval forms and the significance of these forms in the developmental history of the group.

> This fact, joined to the definite character of the changes which make up the life history of a marine crustacean, renders these animals of exceptional value for study of the laws of larval development, and for the analysis of the effect of secondary adaptations, as distinguished from the influence of ancestry; for while Claus has already clearly proved that adaptive larval forms are much more common among the Decapods than had been supposed, his writings and those of Fritz Müller show that no other group of the animal kingdom presents an equal diversity of orders, families, genera, and species in which the relation between ontogeny and phylogeny is so well displayed, but, while proving this so clearly, Claus' well known monograph also shows with equal clearness that this ancestral history is by no means unmodified, and that the true significance of the larval history of the higher Crustacea can be understood only after careful and minute and exhaustive comparison and analysis.[113]

To encourage further the research, Brooks included literature surveys of work done on Crustacea in all his published papers. On one occasion, Brooks even published a paper in Science in which he presented recent work done in Germany on the phylogeny of the group.[114] The article was essentially an abstract of a paper published by the German morphologist, J. E. V. Boas (1855-1935), that offered supplemental information to the work of Müller, Huxley and Claus.[115] Brooks's purpose in printing the abstract was to make available to the American audience the essential points of Boas's publication, which were important for the phylogeny of Crustacea, without the attendant difficulty due to the language and detail of Boas's article.

Brooks's second contribution to the crustacean work was the active encouragement of his students to study particular organisms that were of scientific significance. With E. B. Wilson, he published, "The first zoea of Porcellana."[116] The paper represented a joint effort to study the poorly-understood early developmental stages of _Porcellana ocellata_. In the summer of 1885, Brooks collaborated with a student, A. T. Bruce, to study the king crab, _Limulus polyphemus_.

> Mr. Bruce and I are giving most of our time to the King Crab, Limulus. This is one of the most interesting of our American animals, and European naturalists have often reproached us that so little is known about it, but there are very peculiar technical difficulties.
>
> About three fifths of all known animals are Arthropods, and limulus is the oldest type of the Arthropods which is represented by living forms, so that a complete knowledge of its life history may possibly give the key to the origin and relationship of considerably more than half of the animal kingdom.[117]

A sketch of their research, "Abstract of researches in the embryology of _Limulus polyphemus_," was published in 1855.[118] Bruce was later to obtain his doctorate for his work on Arthropoda. Brooks's own unpublished work on the reptantion decapods (Macroura), which he worked on from 1879-1885, was given to F. H. Herrick to work upon. This resulted in an impressive monograph by Herrick, with an introduction and a preliminary section by Brooks, describing the

Atlantic genus Alpheus for the first time.[119] No less than six of Brooks's students did their graduate research on various problems associated with Arthropoda development.

5. Coelenterate research

The last major area of Brooks's research involved work on Coelenterata. Like much of his other research areas, the initial portions of this work involved the proper identification of various genera. When Brooks originally established the CZL at Beaufort, there were very few sources available to aid in the identification of local marine organisms. For the hydromedusae (the coelenterate class, Hydozoa), John McCrady and Alexander Agassiz had compiled a list of species found in the Charleston region. During the summers of 1880 and 1881, Brooks systematically compared the Beaufort species and the Charleston forms. The result of this effort was that Brooks corrected many observations of McCrady and Agassiz. The corrections usually involved identifying forms that had been accorded the status of a new genus or species, as phases in the life history of existing genera or species. Other species identified by McCrady and Agassiz were verified by Brooks and provided with a complete life history.[120]

Many of Brooks's hydromedusae studies followed the approach he originally took with the Beaufort hydroids. In 1884 he published an article in Zoölogischer Anzeiger on the life history of Eutima mira, as a supplement to material on the species previously published by Claus. In 1888, he described the life history of a new species, Epenthesis mc Cradyi, utilizing microscopical examinations of sections from the species' germ layers.[121] A new hydrozoan genus, Dichotomia, was identified in 1903.[122] Work Brooks initiated in 1886 on Turritopsis nutricula, was continued in collaboration with the student, Samuel Rittenhouse, and completed in 1907 to provide a complete account of the life history of the species.[123] Other hydroid work involved observations upon medusoid forms that reproduced asexually by budding,[124] the demonstration that some coelenterate asexual buds passed through the parental phylogenetic history in their own ontogeny,[125] the microscopical examination of sensory organs of Laodice to confirm observations by the Hertwig brothers tracing the development of the organs to primitive endoderm,[126] and a sectional analysis of the structure and development of the gonophores of particular siphophores to revise work of Haeckel.[127] Much of this work involved meticulous examinations of sections of the hydromedusae to determine the exact germinal origin of specific structures.

Brooks's most important work on hydromedusae was the direct result of many of his investigations of the life histories of several species. The hydromedusae represented a very interesting group to study for Brooks because of the extreme variability in life history exhibited throughout the group. Some species develop through larval forms, others involve both polyp and medusa forms and others utilize both sexual and asexual reproductive strategies. Brooks's immediate interest became the alternation of generation illustrated by certain hydromedusae;

that is, what was the phylogenetic significance of alternation of generation?

In his early work to correct McCrady and Agassiz, Brooks studied the life cycle of Cunocantha octonaria and Turritopsis nutricula. Both species had been previously described as exhibiting alternation of generation. However, Brooks demonstrated that while T. nutricula had such a complex life history, C. octonaria actually did not alternate. Instead, it passed from the egg to a Cunina larval form which had the power of asexual multiplication. The larva could form other larvae, but did not give rise to the medusoid form by budding. The conversion from the larva to the adult was direct. Therefore, since each Cunia larva could produce only one adult by direct metamorphosis, there was no alternation of generation in C. octonaria.[128] From this life history, Brooks theorized that alternation of generation had its origin through a modification of metamorphic generation. The ancestral form of development was direct through a Cunina larval stage. C. octonaria represented only a slight divergence from this primitive plan since the larval stage could asexually produce other larvae.[129]

Brooks's full statement on alternation of generation was published in an impressive and influential article in 1886.[130] The paper was a carefully organized, well-documented attack on the prevailing opinion concerning the origin of the medusoid form and the significance of alternation of generation. Brooks stated that the common opinion of naturalists was that the free sexual medusae form originated from a sessile hydroid, the primitive form.[131]

The medusae were derived as a gradual specialization of the reproductive members from what was called the "polymorphic hydroid cormus."[132] However, the prevailing view had recently come under reexamination from R. Böhm (n.d.) and Claus. Böhm held that the medusae originated from some pelagic form rather than a fixed hydroid. Claus claimed the medusae was older than the "hydroid cormus," the hydroid form was the larval stage of the medusoid form and alternation of generation had its origin through the asexual reproduction of the larvae.[133] Brooks stated that he shared the conviction of Böhm and Claus, but that his own opinion was based on research not available to these two investigators.

> I may be allowed to state that I was led, several years ago, by the study of the development of the Trachomedusae and Narco-medusae, to the conclusions which are here given, before I was aware that Böhm and Claus had also arrived at the same view of the relation between the medusae and the hydra.[134]

Brooks followed this introduction with extensive life histories of Cunocantha octonaria (Narcomedusae), Liriope scutigera (Trachomedusae), Turritopsis nutricula (Anthomedusae) and Eutima mira (Leptomedusae).[135] Each species was described in detail with special attention given to a careful narration of the developmental history of the species. In many cases, Brooks's observations provided corrections and additions to the previous work on the species. In all cases, the previous work was dutifully noted. Brooks then compared the various life histories, beginning with Liriope. This hydromedusae had direct development from the egg through a planula larva to the medusoid adult. Cunocantha offered a modification since the actinula larval form was capable of asexually multiplying to form other larval hydroids before metamorphosing to adult medusae. In Turritopsis, the planula became modified to form an embryonic hydra which formed, by budding, fully developed hydra which produced medusae by budding. Eutima offered yet another modification in that the embryonic root asexually produced nutritive hydra which asexually produced a blastostyle which then budded asexually to produce the medusa.[136] The four life histories illustrated the increasing complexity from Trachomedusae and Narcomedusae to the Anthomedusae and finally, the Leptomedusae.

Brooks also concluded that the life histories of these four species provided the evidence against the prevailing views concerning the origin of the medusea and the origin of alternation of generation.

> The direct conversion of a ciliated, mouthless planula into the tentaculated stomatous hydra will, without doubt, be recognized as the primitive life-history; and the alternation of generations between the planula, or the root into which it becomes converted, and the hydras formed from it by budding, will, I think, be universally accepted as a secondary modification. I shall give, in the last section of this paper, my reasons for believing that the alternation of generations between the hydra and the medusa is not primitive but secondary, and that originally a tentaculated hydra-like larva became directly metamorphosed into a single medusa . . .[137]

Brooks went on to state:

> I think that we may safely conclude that while the view that the complex structure of the medusa has been acquired as a means of distributing the species seems at first sight to be very plausible, more careful examination renders it probable that this is not the case, but that the purpose of the organization of the medusa is to enable it to live out its own life; that it has been acquired and preserved on account of its direct benefit, rather than from any indirect advantage to the species as a whole.[138]

It was just such a "careful examination" of the hydromedusae that enabled Brooks to demonstrate effectively that the planula larva or hydra was the ancestral form of the group and not the medusa. Furthermore, his comparative life history work was convincing in showing that alternation of generation was a secondary modification, first appearing in the hydromedusae larval stage. As a result, the prevailing opinion that the sessile community was the primitive form was replaced by the conclusions of Brooks's work.[139]

6. Methods of research

Brooks's research upon the hydroids marked the final group upon which he carried out a systematic research program. Outside of two papers, one on the life history of Phoronis architecta[140] and the other on bilateral symmetry in starfish larvae,[141] his scientific publications were restricted to work on Mollusca, Brachiopoda, Chordata (Urochordata), Arthropoda (Crustacea) and Coelenterata (Hydrozoa). The work was further limited in that to a large extent all was published prior to the mid-1890's. Both characteristics were directly attributable to the CZL. The location of the summer marine laboratory in the Chesapeake region, at Beaufort, at Woods Hole and occasionally in the Bahamas, was conducive to examinations of the organisms Brooks investigated. With the exception of the echinoderms, which are not as common in areas of soft substrata where the CZL was usually situated, the five groups represent the majority of the marine organisms indigenous to those areas.

It is also noteworthy to mention that essentially all Brooks's scientific papers were published as a result of the work he accomplished at the CZL. This fact becomes more important in understanding the lack of research publications following the mid-1890's. Owing to his own health problems and, in a more severe sense, to those of his wife Katharine, Brooks was able to attend only the CZL in 1891 (Jamaica), 1894 (Beaufort) and 1896 (Jamaica). In 1897, the Johns Hopkins party at Jamaica was struck by yellow fever, with two members of the group succumbing to the disease.[142] Subsequently, the trustees of the University refused to appropriate any further funding. Marine research was still carried out by Johns Hopkins' students at Beaufort, but Brooks did not attend;[143] his wife was so seriously ill that he spent the majority of his time with her. After her death in 1901, Brooks own health began to fail to the extent that he was unable to attend any of the sessions. The exception to this was in 1905 and 1906 when Brooks traveled to the Dry Tortugas upon the invitation of Alfred G. Mayer (1868-1922), to study tunicates. It is significant that these final two trips provided enough new research upon the pelagic tunicates and a species of hydromedusae to allow Brooks to again publish results of his research.[144]

Despite the fact that for the last third of Brooks's career he was unable to conduct the kind of research needed to maintain his impressive early rate of publications, his work between 1876-1896 provides an imposing example of nineteenth-century morphological investigation. Since much of this work was conducted at one of

America's earliest marine laboratories, it is not surprising that many of the forms Brooks studied were virtually unknown to the scientific community. Those that had been previously described had often not been studied in detail or had not been examined correctly. These problems were compounded by the almost complete lack of any authoritarian source for the identification of marine organisms. Brooks's initial task was to provide the necessary descriptive taxonomy to facilitate the marine work.[145]

Many of Brooks's publications of his research were completely descriptive. Much of this work was directed toward providing essential information bearing upon the life history of a species. As a result, Brooks often studied the developmental stages of a species, as evidenced by the _Lingula_ work or the _Ostrea_ research. Or, careful studies were made of specific larval stages in development, as illustrated by the _Lucifer_ and _Squilla_ studies. In several projects, his hydromedusae work serving as the best example, Brooks investigated the species in its complete life history, from the egg to the adult. In all this work, Brooks paid careful attention to detail. His observations upon many marine organisms are striking for the accuracy of the descriptions. To these observations, he often appended considerations of the natural history of the species. The result of such a painstaking organismic study was that he was able to offer life histories of species that clarified previous confusion, accurately described new species and provided the necessary background work for future study.

Brooks's early observational work, epitomized by the studies on Salpa in the late 1870's, primarily involved naked eye examination or low magnification microscope work. The early work on molluscs and brachiopods was much more dependent upon the use of the microscope, requiring magnification in the range of 100-250 diameters (the Lingula work utilized 740X). This latter work also necessitated sectioning the specimens, since Brooks was primarily interested in observing whether the developing gametes within parental tissue or the internal changes within the developing organism. The biological laboratory at Johns Hopkins had been well-equipped at its founding to accommodate such research. The latest Zeiss microscopes with magnification power of up to 1700 diameters had been purchased in 1876. For the sectioning work, there were eight microtomes, two of which were recently developed and manufactured by Zeiss.

The techniques for this study were probably learned by Brooks while he was at the MCZ for in 1876 Michael Foster and F. M. Balfour published the Elements of Embryology, in which the technique for sectioning a specimen utilizing supportive media was explained.[146] The usual method was to coat the material under investigation with paraffin, beeswax or soap and then to slice the specimen into the desired sections. Brooks also learned to use Flemming's fluid as a fixative prior to sectioning to prevent autolysis of the sectioned material.[147]

Following this early work, Brooks's research methods utilizing microscopical observations provided a parallel with developments in cytological techniques. In the late 1870's, all the work was done with simple fixatives such as osmic acid, superficial support for sectioning, carmine stains and conventional optical techniques.[148] As an illustration, Brooks's work on Loligo utilized osmic acid and carmine. The oysters he prepared for sectioning in 1878 and 1879 were fixed and hardened with chromic acid. These techniques were superceded by innovations in the 1880's. Many of these developments dated from the 1870's, but it was not until the eighties that they became fused to the standard cytological methodology. In addition to Walther Flemming's (1843-1905) improvements in a standard fixing agent (1877, 1882), the application of homogenous immersion objectives by Zeiss in 1878 had increased the range of magnification.[149] Work by Paul Mayer (1848-1923) and Martin Heidenhain (1864- ?) on the use of carmine and haematoxylin stains increased the efficiency of staining procedures enormously. Finally, at the Zoological Station in Naples, several investigators began experimenting with placing whole specimens in a paraffin mixture prior to sectioning. This allowed the workers to position precisely delicate, small embryonic forms of invertebrates under examination.[150] In this manner, the precise plane of the section could be accurately controlled. The next step taken at Naples was to develop a technique in which each section that was sliced was united with the previous section. This allowed the preparation of a serial arrangement of a sectioned organism. Thus, the continuous microtome or rotary microtome was applied to research.[151]

The 1880's exhibited a dramatic growth in cytological work due to the three major developments of refined methods of staining, new techniques in sectioning and the innovation of the immersion lens. This same increase in sophistication in microscopical research was illustrated in Brooks's work. In his Salpa study of 1882, Brooks consulted with several anatomists at Johns Hopkins and a local physician, Dr. Bermann, to obtain the latest methods in section preparation. Much of the value of this work was due to the facility of sectioning that the new techniques allowed. Brooks was able to correct previous errors since the long-tailed chain forms of the salp could be arranged in such a manner that longitudinal sections of the whole organisms could be made. These longitudinal sections could then be compared with the transverse sections that were normally prepared, to obtain better resolution of the cells under investigation.

The 1893 work on the salps included several new observations utilizing the right-angle technique of longitudinal and transverse sections. Brooks also experimented with differential staining strategies to obtain more accurate distinctions between cell types.

> In carmine specimens, in which both cell and nucleus are deeply stained, one of these cells might be mistaken for a degenerating egg nucleus, but in good haematoxylin specimens, the larger ones, which are almost as large as the egg nuclei, are seen to be not nuclei but cells . . .[152]

By using carmine and haematoxylin, Brooks was able to point out that the "nuclei" others had described as a degenerating egg or migratory follicle, was, in fact, a complete cell that served as a nutrient source to other eggs.

A later paper, published in 1905 with R. P. Cowles, provides another example of the application of new methods in Brooks's laboratory.[153] For fixative, the chemical used depended upon the specimen to be sectioned. Eggs were fixed with a saturated solution of corrosive sublimate and two percent acetic acid or Perenyi's fluid, with "more valuable" results obtained with the latter.[154] Segmentation stages were specially treated with five percent formaldehyde because this method increased blastomere separation, thereby providing the investigator with a better view of the individual cells. The actinotroch stage was fixed in Perenyi's or Flemming's but it was found that a small amount of four percent muriate of cocaine in fifty percent alcohol when added to the fixative prevented the unnatural bending of the preoral lobe of the larva.[155] For staining purposes, Heidenhain's iron haematoxylin was used for adult sections, with secondary staining provided by alcoholic eosin or rubin. This strategem required very thin sections and produced a marked light-dark contrast between the cytoplasmic material and the nuclei. The eosin and rubin provided secondary stains that could be carefully controlled by the microscopist.[156] Earlier stages of development were stained with safranin in anilin water, which stains only the nuclei. The sections from both young and adult Phoronis that Brooks and Cowles prepared, varied in thickness from two to three microns.

The increasing complexity of histological preparation as evidenced in Brooks's microscopical work from 1880-1908, provided testimony to the many innovations that had taken place in cytology.

It also illustrated Brooks's own awareness of these developments and his application of these new methods to his own research and other studies carried out in the Biological Laboratory. Beale's carmine, the general-use stain of the early 1880's, was gradually augmented with more specific, easier to use and quicker acting stains in the late 1880's and 1890's. Brooks's own research offered an example of the increasing sophistication of the studies. This is clear if one compares the early cephalopod and gasteropod research with the later work on _Salpa_ and _Phoronis_.

7. Brooks as a nineteenth-century scientist

Brooks's research that emphasized the application of microscopical studies of the developmental stages of many invertebrates has led to the characterization of his work as "invertebrate embryology."[157] However, by categorizing Brooks's work in this specific sub-discipline of biology, an inaccurate impression of his role in the late nineteenth century can be obtained. It must be remembered that Brooks's appointment to the Biology Department at Johns Hopkins was made to provide a morphological balance to Martin's physiology program. In 1876 morphology was represented by the study of animal form to identify the unifying relationships between diverse groups.[158] It was in this enterprise that Brooks's research program must be understood. The emergence of distinct sub-disciplines such as invertebrate embryology was a characteristic of the very end of the nineteenth century and, therefore, could not be accurately applied to Brooks.

As a nineteenth-century morphologist, Brooks came under influence of the two dominant traditions in biological thought. One theme was epitomized by the work of Louis Agassiz and the other position was best represented by Charles Darwin.[159] Both of these traditions were very much in evidence in the exact nature of Brooks's scientific work. In a real sense, therefore, his research reflected his nineteenth-century background. Brooks's concern with studying the early stages of the development of organisms to determine the life history of a species can be described accurately as stemming from his association with Agassiz and his training at the MCZ. The application of the facts from these studies to larger questions involving the ancestral heritage of large groups of organisms, reflected Brooks's adherence to the Darwinian program that sought to demonstrate the descent of species. In this regard, Brooks exhibited the prevalent concern of most American naturalists for the application of developmental phenomena to evolutionary morphology.

According to Agassiz, ". . . Embryology furnishes the most trustworthy standard to determine the relative rank among animals."[160] Brooks adopted a similar position by stating that embryology was the only remaining record of the past history of a species' ancestry.[161] Morphology could, however, also use evidence from comparative anatomy and the study of the natural history of the organism to trace the ancestral relations of the species when this material was available.[162] If all this evidence was synthesized, a more accurate description of the phylogenetic history of the organism could be obtained.

> Biological evidence based on embryology and anatomy and on the habits and affinities of animals is justly regarded, by zoologists at least, as a more perfect record of the early history of life than paleontology, and we accept, without questions, proofs of phylogeny which refer to a time very much more remote than the age of the oldest fossils.[163]

The basis for modern morphology, according to both the tradition associated with Agassiz and Brooks, was the doctrine that homologies between organisms provided the exact criterion for the relatedness of those organisms.[164] Homologies existed between species that shared the same similarity of plan or form. By emphasizing the study of homologies to determine relationships, Brooks recognized that investigations of development or embryology were most important. For example, in his work, "The development of the squid," Brooks noted that the cephalopod was the most highly developed invertebrate. Secondary modifications of the embryonic life and adult form of the squid had complicated the life history of the organism to such an extent that the phylogeny was unclear. But, early stages of the squid illustrated a clear homology between cephalopod structures and similar structures in the typical mollusc embryo.

> The only basis for an homology of the Mollusca, in the absence of a phylogenetic record, and of transitional forms, is therefore to be sought in the comparison of early stages in the development of individuals of the different groups, at a time when the specializations of structure, characteristic of the adult form, have not yet made their appearance.[165]

Homologies existing between the ontogeny of two different species, as a result, was indicative for Brooks of the relationship of the forms.

Nevertheless, while Brooks stressed investigations of the developmental stages, evidence from other sources was important. In many cases, such as the later ontogenetic stages of selected cephalopods, the development of a species had undergone modifications that blurred the ancestral relations.

> I shall have to refer again further on to the nature of the evidence from embryology, but I think all morphologists agree that where organs or animals which are shown by their ancestry to be homologous, differ in their ontogeny, we have good ground for expecting to find evidence that the ontogeny has undergone secondary modification and that very considerable embryological diversity is quite compatible with close systematic affinity.
>
> On the other hand, when two animals whose anatomy does not forbid comparison exhibit striking ontogenetic resemblances, there must be held to be evidence of phylogenetic relationship.[166]

Therefore, the morphologist had to exhibit extreme care in applying the evidence from embryology or anatomy to questions of phylogeny. The lack of corroborative evidence in either approach did not negate the observations from the other enterprise.

Brooks's scientific work demanded close attention to any kind of information that might have a bearing upon the phylogenetic history of the species. In the Genus Salpa, Brooks adopted the conditions for morphological and phylogenetic work that were put forward by Anton Dohrn.[167] Under this program, the morphologist was encouraged to establish a direct connection between morphological studies and facts from physiology and other related areas of biology. It was necessary to know the mode of life of the species to augment morphological information from anatomy and embryology.

> The homologies which are established by comparative anatomy, and the primitive identities which are established by comparative embryology are only the means for this end

> [phylogenetic study]. They are in themselves valuable in phylogenetic inquiry only so far as they furnish us the opportunity to pass from consideration of the structure of organs as they now exist, and of the functions of these organs at the present time, to the consideration of conditions which have passed away; to the study of the history of the modifications which have come between the structures and functions and those which we must attribute to the same organs at an earlier genealogical stage.[168]

Brooks assumed this position in the Salpa work. The structural conditions of the tunicates were considered in relation to the conditions of life to determine which functions could be attributed to ancestral heritage and which were due to adaptation to the external conditions.

Unlike his mentor, Agassiz, Brooks believed that the ancestral relationships that were evidenced by comparative embryology, comparative anatomy and the habits and affinities of organisms, were genetic relations. As such, the embryological record could be used as an historical tool to develop the genealogy of a species or group of organisms. The change from the static view of groups of organisms to the historical and evolutionary view of the species that characterized the last half of the nineteenth century, was attributed to Darwin.

> During the last half-century natural science has become historical. We have opened and learned to read a new chapter in the records of the past. The attributes of living things, which seemed to the older naturalists to be complete and independent in themselves, have proved to have a history which can be studied by the methods of science. They have been found to be steps in a long sequence of events as orderly and discoverable as the events which are studied by the astronomer or the geologist.[169]

The adoption of the species as an entity with an historical record led to the construction of classification schemes based upon the descent of species from common ancestors or ancestral forms. These "natural" systems provided the genealogy of a species based upon actual genetic relationships to related forms. Brooks was an early adherent to this view. In a paper published in 1876, Brooks detailed the real connection between the Brachiopoda and Mollusca as stemming from their shared ancestry of a common vermian stock or "trochifera" form.[170] The evidence of the common genealogy was due to a careful study of the embryonic history of both groups. Such an investigation was crucial since the "embryo comes to be left as a sort of picture, preserved by nature, of the ancient and less modified condition of each animal."[171] These facts were sufficient, according to Brooks, to overthrow the belief "so firmly supported by nearly all zoologists a few years since" that all the branches of the animal kingdom are independent. The coup was accomplished by the "constantly increasing tendency" of naturalists to view the facts of embryology and anatomy in terms of evolution theory.[172]

Many of Brooks's studies on the life history of organisms subsequent to the paper detailing the shared ancestry of molluscs and brachiopods, utilized Brooks's careful research to develop genealogies of the groups. In addition to an hypothetical ancestry for the Mollusca, Brooks developed similar schemes for the tunicates, hydromedusae and portions of the crustacean class. It was this type of work that came to characterize morphology following the publication of Darwin's Origin of Species. Brooks realized that there were problems to this research strategy.

> The imperfection of our present knowledge cannot, however, be fairly urged to restrain us from making as much use as possible of what knowledge we do possess, although we must constantly bear in mind that it introduces an element of uncertainty into all of our conclusions. This, of course, is true of all biological speculation at present, but no one would advocate the abandonment of all speculation and comparison until all the facts of our science have been recorded and verified.[173]

Genealogies, therefore, were admittedly speculative in nature and, consequently, somewhat suspect. But it was precisely this imperfection that called for further research to accumulate "all the facts of our science."

Brooks's research was definitely programmed to add the needed details to verify the more speculative ideas of morphology. Using the tools, practices and methodologies that were typical of the late nineteenth century, Brooks investigated questions of developmental history and probable lines of descent. In much of his work, he sought to verify the research of other morphologists. In other areas, he provided novel facts for life histories. In all of this work, it was characteristic of Brooks to exhibit caution in the absence of the necessary factual material. Thus, Brooks commented as follows on the status of molluscan research and its bearing on the phylogeny of the Metazoa.

> As long as the homology of the germ-layers and of the structures derived from them in the subordinate groups of Metazoa remains in uncertainty, any general hypothesis as to their homology throughout the entire group of Metazoa is clearly premature, and I do not think any one who is acquainted with the recent literature on the development of Mollusca will dispute the statement that our knowledge of the mode of origin of the endoderm, the digestive cavity, the mouth and the anus in the various groups of the Molluscs is at present too fragmentary and inconsistent to admit of any general comparisons.[174]

In spite of the attendant hazards, when armed with enough data, Brooks did offer deductive inferences concerning the ancestral heritage of species. It was in some of this work that Brooks illustrated his adherence to the dominant themes of evolutionary morphology. In the Genus Salpa, the impressive monograph which was published near the end of Brooks's active scientific career,[175] he marshalled evidence from paleontology, embryology, anatomy and the habits of organisms to support his contention that the majority of the groups of animals had a pelagic ancestry. By examining the salps, there was evidence of this.

> Embryology also gives us good ground for believing that Salpa follows the analogy of all the metazoa in its still more remote descent from a small and simple pelagic ancestor, and there is good ground for believing that the earliest metazoa were all pelagic, and that they were represented at a very early period in the history of life by floating or swimming animals of minute size and simple structure.[176]

Further evidence came from the nature of the pelagic fauna.

> When all the members of a great group have a definite pelagic larval stage which adheres to the same plan of structure in all of them, we may be pretty confident that this larva is the representative of a primitive pelagic adult animal even if this ancestor has now no unmodified descendants.[177]

In addition:

> Most of the great types of animal life show by their embryology that they run back to simple and minute ancestors which lived at the surface of the ocean and that the common meeting point must be projected back to a still more remote time, before these ancestors had become differentiated from each other.[178]

While Brooks believed the pelagic ancestry of all Metazoa was an accurate hypothesis, he recognized that this reconstruction was purely imaginary and based upon indirect evidence.[179]

Furthermore, this hypothesis had nothing to do with the origin of life, a question Brooks felt was "absolutely unknown at present."[180] Nevertheless, by combining all the factual information available, the morphologist

> . . . does not check the flight of his scientific imagination here, however, for he trusts implicitly to the embryological evidence which teaches him that still farther back in the past all echinoderms were represented by a minute floating animal which was not an echinoderm at all in any sense except the ancestral one, although it was distinguished by features which natural selection has converted, under the influence of modern conditions, into the structure of echinoderms. He finds in the embryology of modern echinoderms phenomena which can bear no interpretation but this, and he unhesitatingly assumes that they are an inheritance which has been handed down from generation to generation through all the ages from the prehistoric times of zoology.[181]

This selection, taken from the Genus Salpa, provides an illustration of the twin influence of developmental studies and evolutionary reconstruction upon Brooks's career work. The fact that the morphologist "trusts implicitly" in embryological data was due to the importance the morphological community placed upon such studies. The early ontogenetic stages of an organism were believed to contain the essential information upon which the morphologist could base phylogenetic claims. The pervasive historical flavor of Brooks's speculations concerning the pelagic fauna can be attributed to his acceptance of evolution theory. Brooks's use of "natural selection" and "inheritance which has been handed down from generation to generation" in the above-mentioned selection supports this claim.

To understand the nature of Brooks's scientific research program and work, one must consider him to be a scientist deeply influenced by the two traditions that primarily influenced late nineteenth-century morphological studies in America. Brooks's general interest in the life history of species stressing the developmental stages and his desire to illustrate the common phylogenetic history of related species exhibited the acceptance of views originally articulated by Agassiz and Darwin. These interests were common among other investigators in American morphology. To understand the success and impact of Brooks's work, one must examine his work vis-a-vis the major questions facing late nineteenth-century morphology. Only in this manner can one understand the specific interests of Brooks's research. In the following chapter, we will discuss the problems Brooks considered and his success in working on these problems.

NOTES

CHAPTER THREE

1. Beaufort was particularly well suited for marine work. As Brooks noted in his report of the CZL for 1880, the area abounded with organisms of great morphological interest. This site became the preferred location for the CZL.

2. Brooks published extensively in Science, Natural Science (London), and Popular Science Monthly during the second period of his career.

3. The morphological component of the work will be largely ignored until Chapter Four, when Brooks will be examined as a representative morphologist. The material in this chapter will be primarily descriptive with an interpretive treatment of the work in the following chapters.

4. W. K. Brooks, "Embryology of the Fresh-Water Mussels," Proceedings of the American Association for the Advancement of Science 24B (1876), pp. 238-240.

5. Ibid., p. 240.

6. W. K. Brooks, "The Affinity of the Mollusca and Molluscoida," Proceedings of the Boston Society of Natural History 18 (1876), pp. 225-235.

7. Ibid., p. 226.

8. Ibid., p. 233.

9. W. K. Brooks, "The Acquisition and Loss of a Food Yolk in Molluscan Eggs," Johns Hopkins University, Studies from the Biological Laboratory 1 (1880), pp. 107-115.

10. Ibid., p. 108.

11. W. K. Brooks, "The Development of the Digestive Tract in Molluscs," Proceedings of the Boston Society of Natural History 20 (1879), p. 325.

12. W. K. Brooks, "Observations upon the Early Stages in the Development of the Fresh-Water Pulmonates," Johns Hopkins University, Studies from the Biological Laboratory 1 (1880), pp. 73-104.

13. _Ibid._, p. 75.

14. _Ibid._, p. 75.

15. E. Ray Lankester, "Observations on the Development of the Pond-Snail (_Lymnaeus stagnalis_), and on the Early Stages of Other Mollusca," _Quarterly Microscopical Journal 14_ (1874), pp. 385-391; Carl Rabl, "Der Ontogenie der Süsswasser-Pulmonaten," _Jenaische Zeitschrift_ 9 (1875), pp. 195-240; M. Ganin, "Beitrag zur Lehre von den Embryonaten Blätter bei den Mollusken," _Warschauer Universitats berichte_ (1873), pp. 115-171; Hermann von Jhering, "Ueber die Entwicklungsgeschichte von Helix. Zugleich ein Beitrag zur Vergleichenden Anatomie und Phylogenie der Pulmonaten," _Jenaische Zeitschrift 9_ (1875), pp. 299-317 and "Ueber die Ontogenie von Cyclas und die Homologie die Keimblätter bein den Mollusken," _Zeitschrift für Wissenschaft Zoologie, März 17_ (1876), pp. 414-433; H. Fol, "Sur le développement des gasteropods pulmonés," _Comptes Rendus 81_ (1875), pp. 523-526. Brooks listed these works at the end of the paper and discussed the problems with each paper in the text.

16. Of interest in this paper is the implicit theme that the investigator could not merely identify a common veliger stage as indicating common ancestry. Brooks's research represented a much more sophisticated approach; that is, one had to observe development from the earliest possible stage.

17. W. K. Brooks, "Observations upon the Early Stages . . .," p. 104.

18. W. K. Brooks, "The Development of the Squid," _Boston Society of Natural History, Anniversary Memoirs_ (Boston: Published by the Society, 1880), pp. 1-22

19. _Ibid._, p. 3. E. Metschnikoff had also written an article on _Sepia_ (1867) and E. Ray Lankester had made observations upon the development of the cephalopods (1875). These works were not cited by Brooks. The works cited were A. Kölliker, _Entwicklungsgeschichte den Cephalopoden_ (Zurich, 1844); H. Grenacher, "Zur Entwicklungsgeschichte den Cephalopoden," _Zeitschrift für Wissenschaft Zoologie 24_ (1874).

20. _Ibid._, p. 16.

21. _Ibid._, p. 17.

22. W. K. Brooks, "The Homology of the Cephalopod Siphon and Arms," _American Journal of Science 20_ (1880), pp. 288-291.

23. Letter, W. K. Brooks to D. C. Gilman, 1878 (early), Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

24. The papers Brooks referred to, all European works, were: T. C. Eyton, History of the Oyster and Oyster Fisheries (London, 1858); Karl Möbius, Die Austern und die Austenwirtschaft (Berlin, 1877); Everand Home, "On the Mode by which the Propagation of the Species is Carried on in the Common Oyster and in the Large Fresh-Water Muscle [sic]," (Croonian Lecture for 1826), Philosophical Transactions of the Royal Society of London (1827), pp. 39-48; J. G. Hart, "Report of the Commission Appointed to Examine into the Methods of Oyster Culture in France and in the United Kingdom with a View to the Introduction of Improved Methods of Culture of the Oyster in Ireland," (1870); Felix Eraiche, Guide Practique de l'Ostreiculture. The list was taken from W. K. Brooks, "The Development of the American Oyster," Johns Hopkins University, Studies from the Biological Laboratory 1 (1880), p. 78.

25. Ibid., p. 3.

26. Ibid., p. 3-4.

27. W. K. Brooks, "Abstract on Observations on the Development of the American Oyster," Zoologischer Anzeiger 2 (1879), pp. 659-660; W. K. Brooks, "Abstract of Observations Upon the Artificial Fertilization of Oyster Eggs and on the Embryology of the American Oyster," American Journal of Science 118 (1879), pp. 425-426.

28. This is the same article as published under the identical title in Johns Hopkins University, Studies from the Biological Laboratory 1 (1880), pp. 1-81.

29. "William Keith Brooks. A Sketch of His Life by Some of His Fromer Pupils and Associates," Journal of Experimental Zoology 9 (1910), p. 3.

30. Letter, W. K. Brooks to D. C. Gilman, May 7, 1882, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

31. Letter, W. K. Brooks to D. C. Gilman, May 25, 1883, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

32. Letter, W. K. Brooks to D. C. Gilman, August 30, 1885, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

33. W. K. Brooks, The Development and Protection of the Oyster in Maryland (Baltimore: Publication agency at the Johns Hopkins University, 1884), p. 5.

34. Ibid., p. 6.

35. Ibid., p. 7.

36. Newspaper articles in the Baltimore American, The Sun (Baltimore), and The Press (Pittsburgh) appeared throughout the 1880's and early 1890's detailing the report of the Oyster Commission and the need for immediate remedial measures.

37. The Nation 53 (1891), p. 57 and Popular Science Monthly 39 (1891), p. 700 carried review articles for The Oyster. Both reviews were favorable to the book as a whole, both recognized Brooks as the foremost expert on oysters, both recognized the problems facing the oyster industry and both were somewhat pessimistic that Brooks's recommendations would be heeded.

38. W. K. Brooks, The Oyster, A Popular Summary of a Scientific Study (2nd edition, Baltimore: The Johns Hopkins Press, 1905), p. ix.

39. Dial 39 (1905), p. 449; Engineering News 55 (1906), p. 192; Independent 59 (1905), p. 1544; Nation 81 (1905), p. 463; and Review of Reviews 33 (1906), p. 125 included reviews of the second edition of The Oyster. Again, these reviews were very sympathetic. Most noted the importance of Brooks's work and the need for the oyster industry to implement the suggestions Brooks offered.

40. Letter, W. K. Brooks to A. M. Mayer, March 7, 1875, Princeton University, Firestone Library Manuscripts Room, Hyatt-Mayer correspondence.

41. W. K. Brooks, "The Affinity of the Mollusca and Molluscoida," p. 234.

42. Ibid., p. 234.

43. Ibid., p. 232.

44. "Chesapeake Zoological Report," Johns Hopkins University, Report of the President (1878), p. 54.

45. W. K. Brooks, "The Development of Lingula and the Systematic Position of the Brachiopoda," Chesapeake Zoological Laboratory, Scientific Results of the Session of 1878 (Baltimore: The Johns Hopkins University Press, 1878), pp. 35-112.

46. Ibid., p. 89.

47. W. K. Brooks, "Du developpment de la lingula et de la position zoologique des brachiopods," Archives de zoologie expérimentale et général 9 (1881), pp. xxviii-xxix.

48. Letter, W. K. Brooks to D. C. Gilman, May 15, 1882, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

49. Tunicates are currently classified as belonging to the phylum Chordata, subphylum Urochordata.

50. Roberta Beeson, "Bridging the Gap: The Problems of Vertebrate Ancestry, 1859-1875." (Unpublished Ph.D. dissertation, Oregon State University, 1978.)

51. W. K. Brooks, "Embryology of Salpa," Proceedings of the Boston Society of Natural History 18 (1875), pp. 193-200; W. K. Brooks, "Embryology of Salpa," Monthly Microscopical Journal 16 (1876), pp. 9-14; W. K. Brooks, "A Remarkable Life History and Its Meaning," American Naturalist 10 (1876), pp. 641-656.

52. W. K. Brooks, "A Remarkable Life History . . .," p. 646.

53. Ibid., p. 654.

54. W. K. Brooks, "Embryology of Salpa" (1875), p. 198.

55. W. K. Brooks, "The Development of Salpa," Bulletin of the Museum of Comparative Zoology 3 (1876), pp. 291-348.

56. Ibid., p. 335.

57. Ibid., p. 336. The Leuckart article, "Zur Anatomie Entwicklungsgeschichte der Tunicaten," Zoologische Untersuchungen 2 (1854), pp. 46-47.

58. Ibid., p. 336.

59. Ibid., pp. 337-338.

60. Ibid., p. 339.

61. W. Salensky, "Ueber die Embryonale Entwicklungsgeschichte der Salpen," Zeitschrift für Wissenschaft Zoologie 27 (1875), pp. 179-237; W. Salensky, "Ueber die Entwicklung der Hoden über den Generationswechsel der Salpen," Zeitschrift für Wissenschaft Zoologie 30 (1878), pp. 275-293.

62. No available biographical information on Bermann nor any information concerning the techniques.

63. W. K. Brooks, "Chamisso and the Discovery of Alternation of Generation," Zoologischer Anzeiger 5 (1882), pp. 212-215.

64. W. K. Brooks, "The Origin of the Eggs of Salpa," Johns Hopkins University, Studies from the Biological Laboratory 2 (1882),

65. W. K. Brooks, "Chamisso and the Discovery . . .," p. 214.

66. Ibid., p. 213.

67. W. K. Brooks, "The Origin of the Eggs of Salpa," pp. 308-309.

68. W. K. Brooks, The Genus Salpa, Memoirs from the Biological Laboratory of Johns Hopkins University 2 (Baltimore: The Johns Hopkins University Press, 1893).

69. Letter, W. K. Brooks to D. C. Gilman, May 3, 1887, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

70. Letter, W. K. Brooks to D. C. Gilman, April 2, 1887, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

71. In a recent article in Scientific American [204(1961):150-160], N. J. Berrill noted that Brooks's work was one of the largest volumes ever published on a single species. More importantly, the work still represents the best description of the Salpa.

72. Review of The Genus Salpa, By W. K. Brooks, in Popular Science Monthly 45 (1894), pp. 272-273.

73. The phylogenetic considerations will be discussed in Chapter Four.

74. W. K. Brooks, The Genus Salpa, p. 55.

75. Ibid., p. 234.

76. Brooks referred to receiving aid from Bermann, Professor William Libbey, Professor L. A. Lee and Bigelow. The latter was a student of Brooks who specialized in tissue preparation.

77. These figures ranged from sketches of the living organisms to sections drawn at 495 diameters. Transverse, horizontal and longitudinal sections were included. A variety of stains were also used. Several of the plates (9, 10, 11, 21, 41, 42) presented details of dividing cells and showed clearly the

dividing nuclei with spindle fibers and mitotic figures. The plates offer an impressive example of the detail Brooks presented in his descriptive work.

78. W. K. Brooks, "The Nutrition of the Salpa Embryo," Johns Hopkins University, Circulars 12 (1893), pp. 97-98.

79. W. K. Brooks, "The Affinities of the Pelagic Tunicates. No. 1. On a New Pyromosoma," Memoirs of the National Academy of Science 5 (1906), pp. 151-156.

80. W. K. Brooks, "IV. The Pelagic Tunicata of the Gulfstream. Part II. Salpa floridana. Part III. The subgenus Cyclosalpa. Part IV. On Oikopleura tortugensis, a New Appendicularian From the Tortugas, Florida, with Notes on Its Embryology," Publication of the Carnegie Institute of Washington 102 (1908), pp. 73-94.

81. Letter, W. K. Brooks to D. C. Gilman, May 4, 1894, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

82. The details of this aspect of Brooks's work will be presented later in this chapter and in Chapter Four.

83. Brooks's research on Lucifer was widely cited in various morphological journals in Europe. In particular, articles and reviews in the 1890's in Zoologische Jahrbücher and Zoologische Zentralblatt concerning crustacean larval development usually referred to the Lucifer work. Brooks was also chosen to examine curstacean samples from the Challenger expedition.

84. Squilla belongs to the order Stomatopoda, subclass Malacostraca of the crustacean class. In the sometimes complicated taxonomy of crustaceans, Stomatopoda is often listed under the section Eumalacostraca and superorder Hoplocarida of Malacostraca.

85. W. K. Brooks, "The Larval Stages of Squilla empusa," Chesapeake Zoological Laboratory, Scientific Results of the Session of 1878 (Baltimore: The Johns Hopkins University, 1878), pp. 145-146.

86. Ibid., p. 146. The papers of Müller and Claus were described in Brooks's article. The citations listed: F. Müller, "Bruchstuck zur Entwicklungsgeschichte der Maulfüsser." Archiv für Naturgeschichte 28 and 29 (1862, 1863) and C. Claus, "Die Metamorphose der Squilliden," Nachrichten von der Konigl Gesellschaften zu Göttingen 6 (1871), p. 169.

87. Ibid., p. 149.

88. Unlike most crustaceans, Squilla does not carry its eggs, but lays them in a burrow. Any attempt by Brooks to raise the eggs successfully in the laboratory proved unsuccessful.

89. W. K. Brooks, "The Larval Stages of Squilla empusa," p. 149.

90. Lucifer is classified under the superorder Eucarida, the order Decapoda, the suborder Natantia and the section Penaeidea (family Sergistidae).

91. Letter, W. K. Brooks to D. C. Gilman, September 8, 1880, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

92. Ibid.

93. W. K. Brooks, "The Young of the Crustacean Lucifer, A Nauplius," American Naturalist 14 (1880), pp. 806-868.

94. W. K. Brooks, "The Embryology and Metamorphosis of the Sergestidae," Zoologischer Anzeiger 3 (1880), pp. 563-567.

95. Letter, W. K. Brooks to Walter Faxon, Feb. [1880), Harvard University, Museum of Comparative Zoology Archives, Miscellaneous manuscripts.

96. Letter, W. K. Brooks to T. H. Huxley, November 30, 1880, University of London, Imperial College of Science and Technology. T. H. Huxley, A List of His Scientific Notebooks, Drawings and Other Papers, Preserved in the College Archives (compiled by Jeanne Pingre).

97. Brooks specifically mentioned that such a publication would be a boost for Brooks's program at Beaufort and it would not place a further burden upon the trustees of the University for financing publishing costs in the United States.

98. W. K. Brooks, "Lucifer: A Study in Morphology," Proceedings of the Royal Society 32 (1881), pp. 46-48.

99. W. K. Brooks, "Lucifer: A Study in Morphology," Philosophical Transactions of the Royal Society of London 173 (1882), pp. 57-137.

100. Ibid., p. 61. Souleyet, Huxley, Hensen, Dana, Semper, Claus, Dohrn and Faxon studied the adult. The only work on the early stages were three sketchy works by Dana, Claus and Willemöes-Suhm.

101. *Ibid.*, p. 65.

102. *Ibid.*, p. 62.

103. The appendages included were: 1st-2nd antennae, mandible, metastoma, 1st-2nd maxilla, 1st-34d maxilliped, pereiopods, 1st-5th abdominal segments, labrum, compound eyes and ocellus.

104. *Ibid.*, p. 115.

105. *Ibid.*, p. 119.

106. The various reports of the *Challenger* expedition were compiled by the foremost naturalists of the nineteenth century.

107. W. K. Brooks, "Report on the Stomatopoda Collected by HMS Challenger During the Years 1873-1876," *Report on the Scientific Results of HMS Challenger—Zoology 16* (1880), pp. 1-114. An abstract was published in *Johns Hopkins University, Circulars 5* (1886), pp. 83-85.

108. W. K. Brooks, "Report on the Stomatopoda . . .," *Circulars*, p. 83.

109. *Ibid.*, p. 84.

110. This became known as "Brooks' Law." Every stage in the larval development was 5/4 larger than the previous stage. Of interest is that the rule is still referred to (see T. H. Waterman, *The Physiology of the Crustacea* [New York and London: Academic Press, 1960]). Brooks's rule provides a satisfactory scheme to analyze the growth of crustaceans within single phases of development, under average conditions. The rule is a consequence of the regular periodicity of physiological processes which govern molting.

111. W. K. Brooks, "Report on the Stomatopoda . . .," *Challenger*, p. 82.

112. *Ibid.*, pp. 23-80.

113. W. K. Brooks and F. H. Herrick, *The Embryology and Metamorphosis of the Macroura* (Baltimore: Johns Hopkins University Press, 1802), p. 326.

114. W. K. Brooks, "The Phylogeny of the Higher Crustacea," *Science 2* (1883), pp. 790-793.

115. The bibliographic entry in *Science* (Ibid., p. 790) for the paper was J. E. V. Boas, "Studien über die Verwandtschafts-beziehungen der Melakostraken," *Morphologie Jahrbücher 8* (1883).

116. W. K. Brooks and E. B. Wilson, "The First Zoea of Porcellana," Johns Hopkins University, Studies from the Biological Laboratory 2 (1883), pp. 58-64.

117. Letter, W. K. Brooks to D. C. Gilman, July 15, 1885, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

118. W. K. Brooks and A. T. Bruce, "Abstracts of Researches in the Embryology of Limulus polyphemus," Johns Hopkins University, Circulars 43 (1885), pp. 2-4.

119. W. K. Brooks and F. H. Herrick, The Embryology and Metamorphosis of the Macroura.

120. W. K. Brooks, "List of Medusae Found at Beaufort, N. C., During the Summers of 1880 and 1881," Johns Hopkins University, Studies from the Biological Laboratory 2 (1883), pp. 135-146 and W. K. Brooks, "Notes on the Medusae of Beaufort, N. C.," Johns Hopkins University, Studies from the Biological Laboratory 2 (1883), pp. 465-476.

121. W. K. Brooks, "The Life History of Epenthesis McCradyi (n. sp.)," Johns Hopkins University, Studies from the Biological Laboratory 4 (1888), pp. 147-162.

122. W. K. Brooks, "On a New Genus of Hydroid Jelly-Fish," Proceedings of the American Philosophical Society 42 (1903), pp. 11-14.

123. W. K. Brooks and Samuel Rittenhouse, "On Turritopsis nutricula (McCrady)," Proceedings of the Boston Society of Natural History 33 (1907), pp. 429-460.

124. W. K. Brooks, "Budding in Free Medusa," American Naturalist 14 (1880), pp. 670-671.

125. W. K. Brooks, "On a New Method of Multiplication in Hydroids," Johns Hopkins University, Circulars 7 (1888), pp. 39-40.

126. W. K. Brooks, "The Sensory Clubs or Cordyli of Laodice," Journal of Morphology 10 (1895), pp. 287-304.

127. W. K. Brooks and E. G. Conklin, "On the Structure and Development of the Gonophores of a Certain Siphonophore Belonging to the Order Auronectae," Johns Hopkins University, Circulars 10 (1891), pp. 87-91.

128. W. K. Brooks, "On the Origin of Alternation of Generation in Hydro-medusae," Annals and Magazine of Natural History 11 (1883), p. 459.

129. Ibid., p. 458.

130. W. K. Brooks, "The Life History of the Hydromedusae: A Discussion of the Origin of the Medusae and of the Significance of Metagenesis," Memoirs of the Boston Society of Natural History 3 (1886), pp. 359-430.

131. This opinion was held by such authorities as Huxley, Gegenbaur, Balfour and Hauman.

132. Ibid., p. 359.

133. Ibid.

134. Ibid.

135. According to late nineteenth-century systematics, the hydromedusae consisted of the orders Narcomedusae, Trachomedusae, Anthomedusae and Leptomedusae. Present day taxonomy differs somewhat. The entire group is listed under the class Hydrozoa. Narcomedusae and Trachomedusae are grouped together as the order Trachylina. Anthomedusae and Leptomedusae are considered to be suborders of the order Hydroida (R. D. Barnes, Invertebrate Zoology [3rd edition, Philadelphia: W. B. Saunders, 1974]).

136. W. K. Brooks, "The Life History of the Hydromedusae," pp. 406-410.

137. Ibid., p. 404.

138. Ibid., p. 421.

139. It is of interest that Brooks's work on the hydromedusae is still considered to be the most accurate.

> In 1886, W. K. Brooks worked out a theory of cindarian evolution that is still supported by many zoologists today. According to Brooks' theory, the ancestral cnidarian form was medusoid, the tendency among hydrozoans has been to suppress the medusoid stage so that, in such forms as hydra, the medusa has completely disappeared. The polyp, on the other hand, represents an evolutionary retention and development of the larval condition.

(R. D. Barnes, Invertebrate Zoology, p. 105.)

140. W. K. Brooks and R. P. Cowles, "Phoronis architecta: Its Life History, Anatomy and Breeding Habits," Memoir National Academy of Sciences 4 (1905), pp. 71-113. This paper is of interest

because of its explicit attempt to clarify the systematics of the phoronid organisms. At the outset, Brooks and Cowles point out the various attempts to align Phoronida with Bryozoa, Brachiopoda, Sipunculida and others. However, the authors do not offer their own interpretation. Instead, they offer a detailed life history of *P. architecta* in an effort to untangle the confused detail of the previous work.

141. W. K. Brooks, "On the Early Stages of Echinoderms," *Johns Hopkins University, Circulars 9* (1891), p. 101. The paper is an abstract of a talk Brooks presented before the National Academy of Science in 1889 reporting on a phase of his research at Woods Hole during the summer of 1889. Utilizing serial sectioning of the starfish larvae, Brooks was able to prove that the water pore and pore canal of the larva are originally bilaterally symmetrical. That is, the larva is originally equipped with a pair of canals. Later developments result in the secondary degeneration of the right canal system. Of interest in the life history of the starfish is that this observation appears to demonstrate that the bilateral condition is ancestral, therefore the bilateral larva must be ancestral. Furthermore, Brooks noted the resemblance between the paired canals of the echinoderm larva and the spiracles in tunicates.

142. Professor J. E. Humphrey, an Associate Professor of Botany and head of the expedition, and Dr. F. S. Conant, a recent Ph.D. from Johns Hopkins and holder of the Bruce Fellowship, were the victims.

143. The U. S. Fish Commission had established, with the encouragement of Brooks, a marine station at Beaufort. In 1898 H. V. P. Wilson, one of Brooks's former students, led a group to Beaufort. When Caswell Grave, another former student of Brooks, was appointed the head of the marine station, which opened officially in 1891, he invited students of the biology department to use the station during the summers.

144. Brooks published only one descriptive article (1903) between 1896-1906. In the final two years of his life, he published six articles. Most of these were upon pelagic tunicates.

145. W. K. Brooks, *Handbook of Invertebrate Zoology* (Boston: Cassino, 1882 and Bradlel Whiddle, 1890). This handbook was designed specifically for work on the marine organisms native to the Atlantic coast of the United States.

146. Sir Michael Foster and F. M. Balfour, *The Elements of Embryology* (London: Macmillan and Company, 1874). This edition contained only information on the chick embryo.

However, the techniques utilized by Foster and Balfour were adopted by most microscopists in the 1870's.

147. Several of Brooks's papers mention the use of Flemming's fluid. He was probably first exposed to this fixative since Flemming's original work was on Anodonta, a species Brooks investigated in the late 1870's. Brooks referred to Flemming's papers in his own pulmonate work.

148. H. J. Conn, The History of Staining (Geneva, N. Y.: W. F. Humphrey Press, 1933), p. 89.

149. Arthur Hughes, A History of Cytology (London: Abelard-Schumann, 1959), pp. 12-13.

150. Ibid., p. 16.

151. Ibid. The preliminary work was by Caldwell.

152. W. K. Brooks, The Genus Salpa, pp. 224-225.

153. W. K. Brooks and R. P. Cowles, "Phoronis architecta," pp. 76-77.

154. Ibid., p. 76. Perenyi's fluid was developed by Josef Perenyi in 1882 utilizing four parts nitric acid (10%), three parts alcohol (90%) and three parts chromic acid (1/2%). The reagent was used widely by Brooks due to its facility in preserving the eggs and embryos in the natural form, with minimal shrinkage and no brittling. [See C. O. Whitman, Methods of Research in Microscopical Anatomy and Embryology (Boston: S. E. Cassino and Company, 1885).]

155. Ibid., p. 156.

156. C. O. Whitman, Methods of Research, pp. 47-48.

157. M. V. Edds, Jr., "Brooks, William Keith," Dictionary of Scientific Biography, ed. by Charles C. Gillespie (New York: Charles Scribner's Sons, 1970), Vol. II, p. 507.

158. Carl Claus, Elementary Textbook of Zoology, trans. and ed. by Adam Sedgwick (4th edition, London: Swan Sonnenschein & Co., 1892).

159. See discussion in Chapter One.

160. Louis Agassiz, Essay on Classification, ed. by Edward Lurie (Cambridge, Mass.: The Belknap Press, 1962), p. 84.

161. W. K. Brooks, Foundations of Zoology (New York: The Macmillan Company, 1899), p. 220.

162. Ibid., p. 310.

163. W. K. Brooks, The Genus Salpa, p. 166.

164. Louis Agassiz, Essay on Classification, pp. 86-87 and W. K. Brooks, Law of Heredity. A Study of the Cause of Variation and the Origin of Living Organisms (Baltimore: J. Murray, 1883), p. 308.

165. W. K. Brooks, "The Development of the Squid," p. 17.

166. W. K. Brooks, The Genus Salpa, p. 131.

167. Ibid., p. 178. Probably Brooks referred to Anton Dohrn "Studien zur Urgeschichte des Wirbelthier körpens," Mittheilungen aus der Zoologischen Station zu Nenpel 8 (1888), p. 76.

168. Ibid.

169. W. K. Brooks, Foundations of Zoology, pp. 140-141.

170. W. K. Brooks, "The Affinity of the Mollusca and Molluscoida," p. 234.

171. Charles Darwin, On the Origin of Species, ed. by Ernst Mayr (Facs. of 1859 ed., Cambridge, Mass.: Harvard University Press, 1964), p. 338.

172. W. K. Brooks, "The Affinity of the Mollusca and Molluscoida," p. 234.

173. Ibid., p. 232.

174. W. K. Brooks, "The Development of the Digestive Tract in Molluscs," p. 325.

175. The Genus Salpa was published in 1893. By this date, Brooks had completed his work on Mollusca, Brachiopoda, Hydrozoa and Crustacea. The only work he conducted after 1893 involved tunicates, with only five papers dealing with other research.

176. W. K. Brooks, The Genus Salpa, p. 144.

177. Ibid., p. 149.

178. Ibid., p. 217.

179. Ibid., p. 148.

180. Ibid.

181. Ibid., p. 219.

Chapter Four: Brooks and Nineteenth Century Morphology

1. Brooks and morphology

In an earlier chapter, morphology was defined as the "science of forms," after Ernst Haeckel. This science involved the twofold approach of the description of the form and structure of an organism, and the elucidation of the ancestral history of an organism. In the last chapter, Brooks was depicted as a morphologist primarily concerned with the descriptive life histories of selected marine organisms. While much of the work of this nature was intended by Brooks to provide the necessary information concerning the life histories of the organisms under investigation, the results of this work often had a bearing upon the ancestral histories of the organisms. In other words, Brooks's scientific endeavors epitomized the dual nature of late nineteenth-century morphology.

For the morphologist, the descriptive aspect of morphology represented a fairly straight-forward approach. In Brooks's case, for example, the summer sessions of the CZL offered many opportunities to describe the life histories of species that had not been studied previously. The methods used were standard. If possible, the eggs of the organism were obtained and fertilized, then development was described through to the resulting adult form. However, the second part of morphology that called for the elucidation of the ancestral history of the organism presented a different problem. While the ontogenetic development of a species was open to scientific observation either <u>in situ</u> or in the laboratory, the phylogenetic development could not be examined in this manner. As a result, the morphologist was forced to develop or to accept a theoretical basis upon which questions of phylogeny could be entertained. It was in this arena of thought that speculation had to supplement empirical data.

In spite of the often hypothetical nature of the ancestral phylogenies, this aspect of morphological study was not without a scientific basis. In 1849, T. H. Huxley demonstrated that many different groups of organisms shared an embryonic stage which consisted of a two-layered form.[1] In this study he suggested that a comparison could be made between the two layers of the coelenterate-type and the germinal layers (ectoderm and endoderm) of the vertebrates. Ten years later, Charles Darwin wrote that comparisons of Huxley's nature that illustrated similar embryonic stages indicated patterns of common descent.

> For the embryo is the animal in its less modified state; and in so far it reveals the structure of its progenitor. In two groups of animals, however, much they at present differ from each other in structure and habits, if they pass through the same or similar embryonic stages, we may feel assured that they have both descended from the same or nearly similar parents, and are therefore in that degree closely related. Thus, community in embryonic structure reveals community of descent.[2]

With Darwin's work, there was a new argument that common embryonic stages represented evidence for a genealogical connection between species. This program was encouraged by Fritz Müller in his book <u>Für Darwin</u> (1864). Müller stressed that embryonic development was the main tool for phylogenetic considerations, especially in cases of direct development from ancestral forms. Kowalewsky's numerous Beitrage (see Chapter One) written between 1866-1869 contributed the most important empirical evidence for the genealogical relationship of different animal groups based upon similarity of germinal layers.[3] He found that the two-layered ciliated embryo was common to many diverse groups. Since these embryonic forms were so similar, one could infer that the structures were homologous. Therefore, homologies of the germinal layers of different types afforded a scientific basis for comparative anatomy and embryology. Ernst Haeckel accepted Kowalewsky's work and expanded upon it in his monumental work, Generelle Morphologie (1866). In this study, the two-layered embryo, or gastrula, was theorized to represent the primitive prototype of the whole metazoan community. From this gastraea, all the groups of Metazoa developed. Since they all shared this embryonic state, it followed that the metazoans shared the same germ layers. Haeckel insisted, therefore, that there existed complete homology of ectoderm and endoderm throughout the whole Metazoa.[4]

By 1880, the view that the germinal continuity of all metazoans represented the community of descent of the group, was widely disseminated and accepted. In the morphological community, this became the foundation upon which phylogenetic considerations were based. The article in Encylcopedia Britannica (1883) entitled "Morphology" stated that this branch of scientific investigation was concerned with classification schemes based upon the reconstruction of genealogical trees. The most valuable work in guiding morphology was Haeckel's Generelle Morphologie.[5] Basing his work upon the Gastrae theory of common descent, he stated it was the morphologist's job to examine the development of each organism from the embryonic layers. This ontogenetic basis for phylogenetic considerations became the guide for morphology.

> A strictly morphological standard must be applied to the construction of classifications and the pruning of genealogical trees; organisms are "higher" or "lower" not according to their stage of evolution in beauty or intelligence but to the degree of morphological differentiation by excess, suppression, or coalescence which they exhibit.[6]

The gastraea-theorie became the standard starting point for the morphological community in the late nineteenth century. Essentially all the major morphologists accepted the common ancestry from a gastraea progenitor or developed some modified form of the hypothesis. Carl Gegenbaur stated in 1878 that the gastraea-theorie was the "fundamental form" of the animal kingdom.[7] Because of the common form inferred germinal homology phylogenetic considerations could be uncovered.

> It is, however, the business of Comparative Anatomy to follow out the changes in the organisation, and to discover what is "similar" in the changed and metamorphosed forms, however deeply hid it may be. . . . Homology therefore corresponds to the hypothetical genetic relationship. In the more or less clear homology, we have the expression of the more or less intimate degree of relationship.[8]

E. Ray Lankester represented the modified response to the gastraea-theorie; that is, he accepted the theory in a modified form. Lankester had conducted numerous observations of embryonic development, principally upon molluscs, and found that Haeckel's views on the complete homology of the gastrula and its mode of origin were not correct. In the gasteropod molluscs, some species have gastrula in which the blastopore becomes the adult mouth while in others the blastopore undergoes secondary modification to form the anus. According to Haeckel, therefore, one would have to accept the homology of the mouth to the anus, a clear problem. Secondly, Lankester noticed that the diploblastic phase of development (gastrula) did not always originate by invagination of the outer layer, but sometimes formed the endoderm by delamination of the outer layer. Because the gastrula could be formed in at least two dissimilar ways that illustrated different origins of the germinal layer, Lankester viewed the gastrula as not representing the primitive condition. In its place he offered the "planula theory."[9] According to this view, the gastrula stage was preceded by a common embryonic form in which the differentiation of cells into ectoderm and endoderm had already been initiated. From this planula stage, invagination, delamination or a combination of these processes formed the gastrula as a secondary modification of the diploblastic stage.

Regardless of whether morphologists accepted or modified the gastrula theory, it did provide the initial groundwork for the phylogenetic questions. In particular, the valuable tool of examining various embryonic forms for homological structures was based upon the supposed germinal continuity of species from a primitive form. Furthermore, it was explicitly believed by the morphological community that ontogeny was a recapitulation of phylogeny. Therefore, the record of the descent from the primitive forms could be obtained by studies of ontogenies. In this manner genealogies based upon a natural system of classification could be drawn up.

There were other major responses in morphology to the Gastrae theory in addition to Gegenbaur and Lankester. F. M. Balfour's influential work, A Treatise on Comparative Embryology was printed in 1880.[10] The work represented a practical modification of Haeckel's work since Balfour believed that in many cases, tracing development back to the gastrula progenitor was not possible. Instead the morphological investigator was encouraged to look for ancestral forms common to large metazoan groups, especially investigating the possibility of common larval types (nauplius, trochophore, planula, etc.).[11] Particular attention was directed toward determining any larval conditions that may have resulted from secondary modifications. Balfour was convinced that phylogenetic schemes based upon ontogenetic studies often were erroneous because certain embryonic stages underwent modification in their adaptation to larval life. Therefore, it was the role of the morphologist to uncover the primitive condition. Only in this way could many complicated ontogenies and phylogenies be explained in terms of community descent.

> It is interesting to note with reference to the larvae of the Echinodermata that the various existing types of larvae must have been formed after the differentiation of the existing

> groups of the Echinodermata otherwise it would be necessary to adopt the impossible position that the different groups of Echinodermata were severally descended from the different types of larvae. The various special appendages, etc. of the different larvae have therefore a purely secondary significance; and their atrophy at the time of passage of the larva into the adult, which is nothing else but a complicated metamorphosis, is easily explained.[12]

In addition to the modifications of the embryonic stages that clouded the ontogenetic picture, Balfour was critical of the Gastrae theory because of its treatment of several major morphological questions. The gastrula theory did not provide any information concerning the differential stages from the compound protozoan to the metazoan; the theory did not deal with the possibility of polyphyletic lines of metazoan descent from the primitive Protozoa; and the theory did not satisfactorily give evidence for the existence of complete homologies between the two primary germinal layers throughout the Metazoa.[13] These problems were coupled with the observations, similar to Lankester, that indicated the gastrula could form from either a process of invagination <u>or</u> delamination, both of which differed in cell-type origin. The result was that the gastrula stage throughout the metazoans were extremely variable and, at best, represented a general ancestral form. Nevertheless, Balfour supported the theoretical basis of questions of ancestry as being based upon the primitive gastrula.

> These conclusions do not, however, throw any doubt upon the fact that the gastrula, however evolved, was a primitive form of the Metazoa; since this conclusion is formed upon the actual existence of adult gastrula forms independently of their occurrence in development.[14]

Balfour's elaboration of morphology called for a sophisticated study of the developmental stages of organisms. Only by comparing the larval stages of related groups could the morphologist uncover which characteristics were primitive, therefore having application to questions of ancestry, and those characteristics which were secondary modifications. This program led to an emphasis upon the study of larval forms to determine the probable character of the prototypic larva and the natural relations of larval forms.[15] By examining the various larval types, Balfour was able to group all larval types above Coelenterata into a ciliated bilateral ancestral form. In addition, he was led to believe that the amphiblastula of Porifera represented the transitional form between Protozoa and Metazoa. For Balfour, the amphiblastula replaced the blastula as the primitive ancestor to the Metazoa.[16]

Adam Sedgwick (1785-1873) was another nineteenth-century morphologist who elaborated upon Haeckel's hypothesis. Sedgwick theorized that a coelenterate-like ancestor was the primitive stock for Coelenterata and the higher segmented animals.[17]

> . . . all the most important organ systems of these Triploblastica are found in rudimentary condition in the Coelenterata; and that all the Triploblastica referred to must be traced back to a common diploblastic ancestor common to them and the Coelenterata.[18]

This hypothesis was based upon the Gastrae theory. As the primitive gastrula increased in size, more surface area was demanded of the gut for proper circulation of nutritive matter. The segmented somites of the metazoans were thus derived from gut pouches which were thought to be homologous with the alimentary pouches of Coelenterata. Sedgwick further believed that the tentacles, pores to exterior, circular muscles and sense organs of the coelenterate were repeated in the segmented ancestor as segmented appendages, nephridia, muscular system and nervous system.[19] This illustrated the triploblastic origin from diploblastic structures. Amphiblastula, the ideal ancestor of Annelida, Arthropoda, Mollusca and Vertebrata, was a common segmented ancestor that was derived from the coelenterate-like stem form.[20]

Continued investigations by morphologists of life histories and their relationship to ancestral heritages in the 1880's began to point out clearly that Haeckel's universal Gastrae theory had serious problems. In particular, the study of the homologies of the germinal layers of different organisms, which provided the scientific basis for comparative anatomy and embryology, revealed that a strict homology of the primary germ layers did not exist throughout the animal kingdom. Carl Claus' test, Elementary Textbook of Zoology,[21] originally published in 1884, was quite critical of the theory.

> It cannot, however, be said that this theory [gastraea theory], which is essentially an extension of the Baer-Remak theory of the germinal layers from the Vertebrates to the whole group of Metazoa, with its pretentious and hasty speculation has created a basis for comparative embryology; such a basis can only be obtained as the result of comprehensive investigations.[22]

The investigations Claus encouraged were conducted with the conviction that the development of the individual was in relation to its phylogeny. Instead of stressing the explanatory value of the Gastrae theory, Claus utilized the "Darwinian principles" and the theory of descent.[23]

> The great series of phenomena which could hitherto only receive a teleological explanation are thus brought into causal relation, and can be explained as the inevitable result of efficient causes, and their natural connection is thus rendered intelligible.[24]

Regardless of the growing skepticism concerning the universality of the Gastrae theory, the importance of examining the germinal layers of the embryo or, at least, the early embryonic stages of development, retained its importance in morphology. This type of investigation had become so intimately associated with the widely accepted theory of descent and the biogenetic law, that problems with the Gastrae theory had little impact upon the embryological work. Indeed, even Claus, who had referred to Haeckel's work as "pretentious and hasty speculation" still looked for embryonic homologies. In the 1880's those studies became more sophisticated. The morphologists noted that the embryonic record had become blurred by ontogenetic adaptations to larval life. The task was no longer to make facile comparisons to a diploblastic ancestor, but to uncover the homologies even if they were restricted to one group. Still, Claus believed, the "whole of Morphology tend to show the correctness of the theory of transmutation of species."[25] The morphologist had only to study the variations of form to discover which was ancestral and which was secondary to see the parallel between individual development and the development of the group.

> This parallel, which naturally presents numerous greater or smaller variations in detail, is explained by the theory of evolution, according to which the developmental history of the individual appears to be a short and simplified repetition, or in a certain sense a recapitulation, of the course of development of the species.[26]

The problem of the homologies of germ layers was not ignored, however, in the 1880's. Despite the growing skepticism with Haeckel's version of the *gastraea*, or maybe because of the increasing problems with the theory, the modifications of the theory that were indicative of Lankester's work continued. One of the major works addressed to this problem was conducted by Elias Metschnikoff (1845-1916).[27] After tracing the development of the germinal theory of ancestry to Huxley's 1849 medusa work, Metschnikoff stated the present problem (1886) of the theory was that the

> genealogy of the germinal layers does not rest on a safe basis, since we know nothing of the primitive condition of the Metazoa.[28]

While the doctrine of descent had been applied successfully to the study of morphology, the transition from the Protozoa to the Metazoa was not clear. The *gastraea* theory was particularly problematical since it failed to explain the multiple formation of endoderm in the embryo. To answer the objections, various morphologists had proposed alternatives to the gastrula: Lankester suggested the planula stage; Balfour opted for an amphiblastula progenitor; Bütschli promoted the ancestral placula. Nevertheless, Metschnikoff viewed all these as failures. His alternative was another universal ancestral form, phagocytella, that had its origin in a protozoan choanoflagellate ancestor.[29] Metschnikoff thought the phagocytella overcame the problems of competing ancestral forms since its ameboid blastoderm cells could migrate to any position within the developing embryo. In short, any variation in endodermic origin could be explained. Nevertheless, Metschnikoff did not offer his view as a dogmatic assertion; it was intended to provide direction for additional research. His monograph concluded with an encouragement to study the primitive condition of the Metazoa to place comparative morphology on a solid base.[30]

While criticisms of and alternatives to the gastraea theory characterized morphological work throughout the 1880's, there remained several adherents to the gastraea theory. Evidence for this came from the work of the morphologist Arnold Lang (1855-1914).[31] In Textbook of Comparative Anatomy he accepted Haeckel's version of the Gastrae theory as indicating a complete homology throughout Metazoa of ectoderm and endoderm. It followed that all Metazoa were descended from the common ancestral gastraea which, in turn, had its origin from the protozoan stock. Lang felt the evidence had been so conclusive in favor of Haeckel that "the Gastraea theory, has been very generally accepted."[32]

This brief review emphasizing the gastrula theory, illustrates several characteristics about the nature of morphological study around the 1880's. Drawing its inspiration from the theory of descent, the biogenetic law and, most importantly for the nature of the work, from various views concerning the germinal continuity throughout the animal kingdom, the work emphasized the developmental history of species. Much of this effort was directed towards discovering homologies that existed between related groups. By determining such relationships it was hoped that the primitive condition of developmental stages could be separated from the obfuscating effects of secondary modifications and adaptations. The more sophisticated these studies became in the 1880's the more critical morphologists became of the gastraea theory. Generally speaking, the gastrula became a general archetype which most morphologists referred to as providing a basis for their investigation. However, in specific terms, the implied homology of all ectoderm and endoderm based on the common Gastrae theory was critically received. In spite of the variety of receptions of the germinal theory of ancestry, the nature of morphology was surprisingly uniform. From the standard textbooks available in the 1880's it is evident that the prevailing theme was the relationship of ontogenetic development to the phylogenetic history of the group. It was standard practice in texts on comparative anatomy and embryology to follow the descriptive treatment of each taxonomic group with a discussion of the ontogeny and phylogeny of the group. Morphology in the 1880's retained its interest in the life history of the organism and the ancestral lineage of the group.

It must be stressed that the studies by morphologists in the 1880's were characterized by extensive detail to the developmental stages or life history of organisms under investigation.

Both in textbooks and scientific publications there was a conscious desire to determine the exact ontogeny of as many organisms as possible. Subsequent to these studies, the morphologists retained their interest in providing ancestral histories. These genealogies drew primarily upon the embryological or homological observations guided by hypothesis and speculation. After all, the morphologist was encouraged in this direction.

> Not only is the student thus taught to retain and accumulate his facts in relation to definite problems which are actually exercising the ingenuity of investigators, but he is encouraged, and to a certain extent trained, in the healthy use of his speculative faculties; in fact the one great method by which new knowledge is attained, whether of little things or of big things--the method of observation (or experiment), directed by speculation--becomes the conscious and distinctive characteristic of his mental activity.[33]

Furthermore, the morphologists felt that the application of phylogenetic speculations was a valuable part of biological investigations. Indeed, such a method allowed one to organize data, to provide valuable contributions to morphology and to point out to others avenues of further research.

> I am aware that by some naturalists speculations as to the affinities and phylogeny of animals are still regarded as worthless and even dangerous; but probably such views will become rarer year by year as biology, by means of theories and reasoning, becomes more and more a true science and less a mere accumulation of facts. I regard phylogenetic conclusions founded upon the structure and developments of the animals as not only most valuable and interesting in themselves, but as exercising an important influence upon the further progress of the science. And I consider that it is the duty of a biologist, who has made a special study of a group of animals or plants, to attempt to express any views he has formed as to their relations in a phylogenetic form. Such theoretical inductions from his observations are most suggestive and helpful to other workers. If his conclusions be correct, they form an important contribution to knowledge; and

> if they be incorrect, they may still be useful in directing attention to points requiring further investigation, and at any rate the errors will soon be discovered and corrected by his successors.[34]

As this quotation from W. A. Herdman (1858-1924) indicates, the morphologist did not consider the phylogenies to be dogmatic, ad hoc speculations. Rather, they were based upon observations and were put forward in a manner to clarify matters of dispute or to encourage research.

While the increasing sophistication of morphological studies in the 1880's called for refinement of the homology concept, it did not create a serious objection to the speculative aspects of morphology. Indeed, some of the most impressive morphological work that was done during this period included ancestral considerations. C. O. Whitman, who was to become a central figure in American biology because of his role in the development of the Marine Biological Laboratory at Woods Hole, conducted several important investigations on annelid development in the 1880's. In "A contribution to the history of the germ-layers of Clepsine," Whitman stated the value of observations upon the development of germ layers to questions of phylogeny.

> Allowing that they [germ layer studies] are correct, it will be seen that they furnish what we have long stood in need of, - a satisfactory basis for the comparative study of the germ-layers in annelids, - and that they give us one more clue to the ancestral history of vertebrates.[35]

E. B. Wilson, one of the most well-known of Brooks students, included similar considerations in his important works on annelids, "The embryology of the earthworm."[36] Illustrating the caution most morphologists took with phylogenies, Wilson stated the following.

> There is reason to believe that Lumbricus is a somewhat specialized form, both anatomically and embryologically, and it is therefore necessary to be cautious in drawing general conclusions from the phenomena of development, especially in respect to their phylogenetic significance. Yet the very fact of secondary modification having taken place gives value to a comparison of the development of Lumbricus with that of other annelids, since it gives in some degrees a test of the weight that can justly be assigned to the various features of ontogeny.[37]

Later ancestral considerations by Wilson again revealed the cautious approach and tenuous nature of such suggestions.

> Further than this I shall venture no conjecture as to the character of the adult ancestral form, except to state that the views suggested are reconcilable with the derivation of annelids either directly from Coelenterata, or from Platyhelminthes, in accordance with the views of Balfour and Sedgwick, or Lang. The essential features of all these views is the identification of the principal or longitudinal axis of the body with one of the transverse axes of the gastrula, and hence of the Coelenterata ancestral type, which the gastrula in some degree represents; and we owe to Balfour the fruitful suggestion that the nervous system of the Bilateralia may have arisen directly by the elongation of the circum-oral ring of the ancestral form.[38]

From the work of Herdman, Whitman and Wilson there is evidence that questions of ancestry remained a central question for morphology at the end of the nineteenth century.

The morphology work of Brooks during this same period reveals his shared concern with most of these characteristics of the morphological community. That the majority of his work dealt directly with life histories of organisms was demonstrated in Chapter Three. The results of these investigations, in characteristic late nineteenth-century fashion, were applied to illuminating the ancestral heritage of the group being studied.

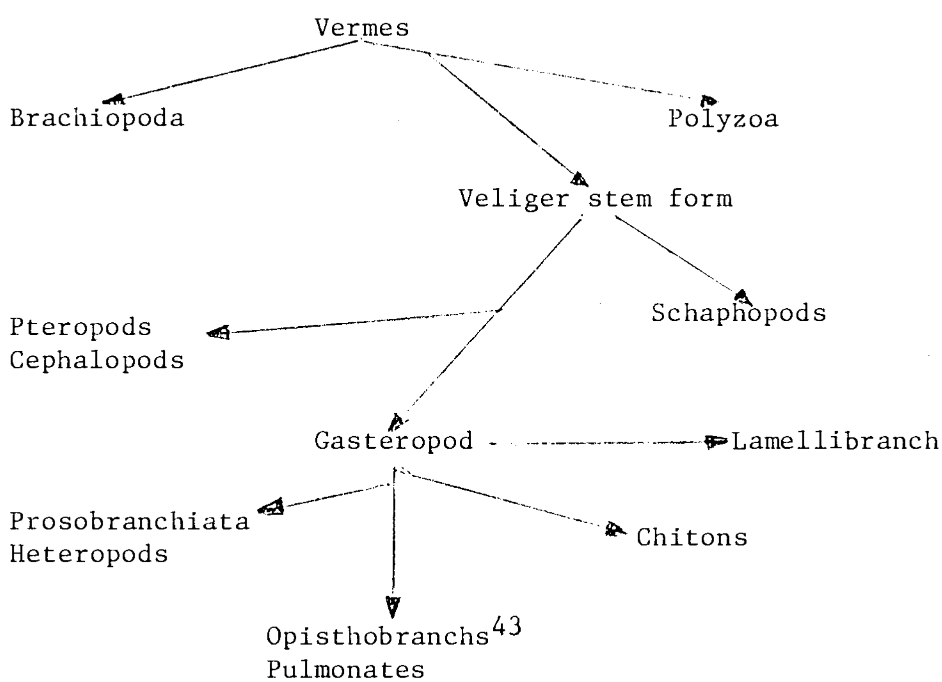
In E. G. Conklin's notes of a Morphological Seminary meeting in 1889, Brooks stated, in the fashion of classical morphology, that the origins of animal form could be sought among any of these sources.[39] These included work in paleontology, comparative anatomy and embryology. However, according to Brooks, "Paleontology offers but scanty evidence" since it usually had little information upon the phylogenetic antiquity of various classes[40] and the crucial transitional forms between taxonomic units were generally missing. As a result, "Evidence from Paleontology is . . . uncertain."[41] Therefore, paleontology had a minimal application, in most cases, to the ancestral history of the group. This fact alone created a serious problem for the morphologist since paleontology offered the only possible direct evidence of ancestry. This led Brooks to state that these ancestral studies were based upon "probability." Nevertheless, the available evidence was valuable.

> The presumption is, therefore, very great that the genetic relations of living things may be expressed with general accuracy by a phylogenetic tree, although the chances of minute accuracy of detail in favor of any particular tree which is drawn up from paleontological evidence are very slight. This lack of minute accuracy can not be urged as an objection to all attempts at following out, in a general way, the lines of evolution of our present groups of animals, according to the best evidence which is attainable, and we must remember that only a very small part of this evidence is furnished by paleontology. If no fossils were known, the facts of comparative anatomy, of embryology, and of geographical distribution would be enough to satisfy us that living things known to us are the divergent descendants of more generalized ancestors, and that their relationships can be most exactly expressed by a system of converging lines, which meet and form larger branches to represent the extinct ancestors from which our divergent species are descended. The evidence is circumstantial, and

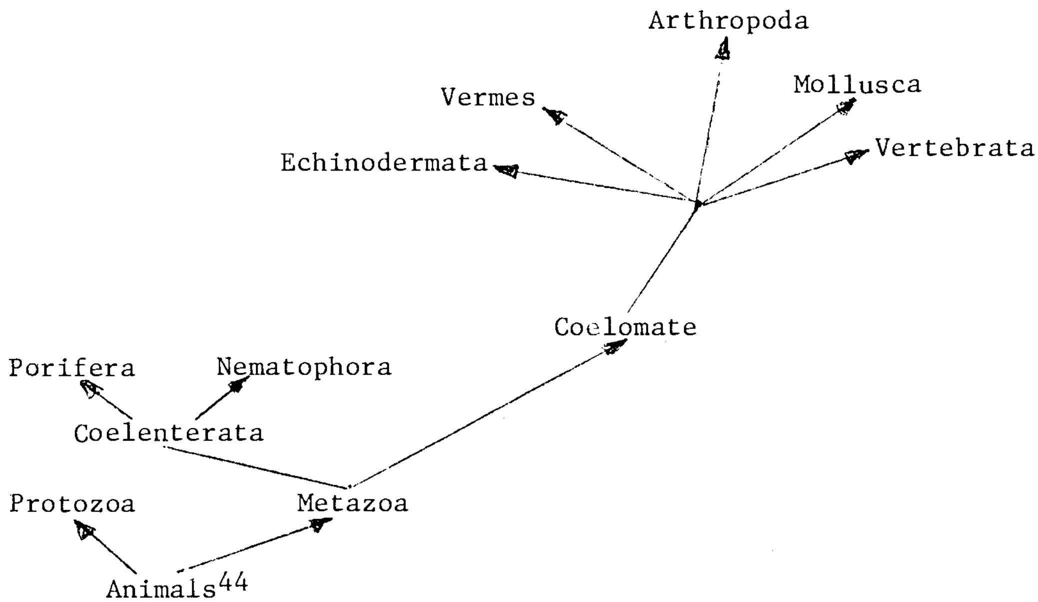
> only leads to general conclusions, and a complete series of fossil forms is the only absolute proof which we could have; but, in the absence of this proof, the conclusions drawn from the study of living animals are rendered extremely probable by the fact that the fossil members of the more modern groups of animals, such as the mammals and birds, are just such forms as the evidence from other sources leads us to expect, and the attempt to read and interpret such records as we have, and to trace the history of life with as much accuracy as possible, is therefore perfectly legitimate, and may fairly claim the attention of the morphologist.[42]

Brooks assumed, therefore, that there was enough evidence to make the tenuous nature of ancestral history "extremely probable."

Like the majority of the late nineteenth-century morphologists, Brooks's studies of the relationships of organisms yielded speculative genealogies, drawn in the standard "phylogenetic tree" mold. For example, Brooks offered the following diagram in 1876, expressing the relationship of <u>Mollusca</u> and <u>Brachiopoda</u>.



A more exhaustive tree was offered by Brooks to his General Zoology class at Johns Hopkins University in 1888.



[44]

In a manner similar to most phylogenetic schemes in the 1880's, Brooks stated that the Metazoa line began with a single-celled organism and passed, in development, through a gastrula-like stage in which all the cells were alike.

Because of the assumed common ancestry of all metazoans, Brooks accepted the developmental history of a species as providing the most important information for probable lines of descent. Thus, in examining the relatedness of two similar forms, the morphologist paid particular attention to embrylogical characteristics.

> The case which we have just examined shows that the embryology of two related forms may be essentially the same since both of them have inherited the greater part of their life-history from a common parent, and it would seem at first sight as if all

> that we need, to enable us to trace out the relationship of all living animals, is a complete acquaintance with the embryology and metamorphosis of each one of them. A comparison of all the stages in the life of one species with all the stages in the life of another species of the same genus ought to show essential identity; and a comparison of the stages of development of the species of one genus with those of the species of a related genus ought to show how far their history has been the same; the common features in the embryology of two allied families should show how far the history of the species in one of them has been the same as that of the species in the other, and so on, each wider and wider comparison showing broader and broader relationships, until the features which are common to the embryos of all animals unite them into one great group.[45]

In Brooks's early career, like many other investigators, he thought that descriptive embryology of all animals held the key to the natural system of classification. The goal was to collect life histories of as many animals as possible. Comparative studies of these histories could reveal the common embryonic stages and, consequently, indicate the ancestral relatedness.

Brooks's work on the developmental stages of various groups revealed to him the problem of embryological data in its application to phylogenies. That is, the ontogeny of the species had been acted upon by natural selection and variation as much as the adult stages of the organism.[46] The result was the modification of the primitive condition to such an extent that it was often difficult to elucidate any ancestral characters. This situation made the morphologist's task even more problematic. Not only did the investigator have to depend upon indirect evidence (direct evidence from paleontology was lacking), but the main arsenal of indirect evidence was often tarnished by secondary modifications.

For the late nineteenth-century morphologist, the only avenue immediately available around the problems of the observational evidence was speculation. In the absence of demonstrated fact, Brooks felt that such reasoning was necessary and valuable.

> The end of phylogenetic speculation is perfectly legitimate, but we must rid our minds of the belief that it can be reached by mere observation and description. The evidence is often so hard to read that the accounts of the best observers are contradictory, and in many cases it is so scanty and incomplete that it must be submitted to a severely critical process of comparison, analysis, cross-examination, and elimination, before a general conclusion can be reached.[47]

Speculations concerning the phylogeny of an organism, in distinction to careful observations upon the ontogeny of a species, were tenuous "theoretical discussion[s]" which could "be very modified or entirely replaced by subsequent discoveries."[48] In fact, this characteristic of these hypotheses made them a valuable incentive for further work, a fact noticed by many morphologists.[49]

In 1893, Brooks detailed the methodology of the morphologist in dealing with questions of ancestry. The following account concerns the echinoderms, but the same method would apply to any animal group.

> The morphologist unhesitatingly projects his imagination, held in check only by the laws of scientific thoughts, into the dark period before the times of the oldest fossils, and feels absolutely certain of the past existence of a stem-form, from which the classes of echinoderms have inherited the fundamental plan of their structure, and he affirms with equal confidence that the structural changes which have separated this ancient type from the classes which we know were very

> much more profound and extensive than all the changes which each class has undergone from the earliest paleozoic times to the present day.
>
> He is also disposed to assume, but, as I shall show, with much less reason, that the amount of change which structure has undergone is an index to the length of time which the change has required, and that the period which is covered by the fossiliferous rocks is only an inconsiderable part of that which has been consumed in the evolution of the echinoderms.
>
> The morphologist does not check the flight of his scientific imagination here, however, for he trusts implicitly to the embryological evidence which teaches him that, still further back in the past, all the echinoderms were represented by a minute pelagic animal which was not an echinoderm at all in any sense except the ancestral one, although it was distinguished by features which natural selection has converted, under the influence of more modern conditions, into the structure of echinoderms. He finds, in the embryology of modern echinoderms, phenomena which can bear no interpretation but this, and he unhesitatingly assumes that they are an inheritance which has been handed down from generation to generation through all the ages from the prehistoric times of zoölogy.[50]

In other words, it was the embryologic record that provided the necessary scientific support upon which the morphologist could speculate. The method involved imagination, but even this aspect of speculation required regulation by the "laws of scientific thoughts."

While no morphologist could deny that an element of his study, namely that portion concerned directly with phylogenetic heredity, contained a speculative aspect, none would admit that the speculations were completely _ad hoc_. Indeed, if one accepted, as the morphologist did, that all metazoans shared a common ancestry, then indirect evidence based upon the embryological record could be brought to bear upon phylogenetic questions. The evidence sought after was the resemblance of embryonic forms of two related species in order to find homological structures.

> . . . we appeal to embryology, and ask whether the resemblance becomes more marked or less marked when we study it in its younger stages. The arm and the wing are more alike in the embryo than they are in the adults, and the features which they share in common make their appearance earlier than their distinctive characteristics.
>
> The homology then is a resemblance which is not due to similarity of use, and which is more conspicuous in the embryo than in the adult.[51]

For Brooks, the basis of modern morphology was the doctrine that homology indicated genetic relationship.[52] In this manner, two forms that gave evidence of closely homologous structures through embryonic developments could be described as sharing a close phylogenetic history.

Brooks grouped homologies under two categories. The first type of homology was general. These homologies existed between different parts of the same organism and were due to the common ontogenetic history the parts had as a result of belonging to the same organism. Brooks used this category most effectively upon segmented organisms, especially in his studies on the crustaceans. The second kind of homology was special. These relationships existed between corresponding parts of different animals and were due to a common phylogenetic heredity. Investigations utilizing special homologies yielded, in most cases, the best information for ancestral histories. However, due to modifications of embryonic stages, these homologies also created special problems for the investigator. In widely modified groups, only the earliest embryonic stages provided any evidence for special homologies. As a result, the quest for these relations demanded an increasing awareness of these early stages. Brooks's own work in the 1880's reflected the more sophisticated approach. In comparing the embryo of the cephalopod Loligo to the common veliger-like gasteropod embryo of the same age, Brooks only referred to very early embryonic structures as sharing homologies. The mouth, velum, sensory tentacles, mantle, shell area and anus were homologous between the cephalopod and gasteropod. However, the previously accepted view that the cephalopod arms and siphon were homologous with gasteropod structures was denied by Brooks because the embryonic evidence revealed they were secondary modifications in ontogeny.[53] His later work emphasized attention to the homologies existing in the gut of related forms since this structure was one of the earliest definable structures appearing in development. For example, Brooks referred to these relationships in echinoderms during a session of the Morphological Seminary.

> Homologies & Analogies of Echinoderms, mid-gut, hind-gut, & sometimes foregut, have passed over from the bilaterally symmetrical larva into adult and are homologous in all echinoderms. Originally the larval mouth become adult mouth in Echinus, as in other echinoderms.
> In Synapta the mouth, wh.[ich] is on ventral side of larva, comes to lie at anterior end of body. Arms originally ventral in bilateral form.
> In asteroids arms may be absent.
> Position of arms is so variable, that it is not of much value for drawing homologies.[54]

His studies of the life histories of various mollusks and hydromedusae paid particular attention to the development of the gut to clarify systematic position.

Brooks's utilization of the concept of homology as the basis of morphology can be attributed to his acceptance of the view of germinal continuity throughout the Metazoa. Undoubtedly this idea can be traced, as it was in Brooks's European counterparts, to Haeckel's Gastrae theory. Brooks often referred to Haeckel's work and included _Generelle Morphologie_ on his graduate student reading list in 1890. However, again illustrating a common character of morphological study in the 1880's, his research demonstrated a growing skepticism to the details of Haeckel's theory.

In Brooks's earliest work on the marine prosobranchs, _Astyris lunata_ and _Urosalpinx cinerus_, during the summers of 1877 and 1878, he noted that following the segmentation of the egg the ectoderm tended to spread over the endoderm and the two layers became separated by a segmentation cavity. He was not able to witness the _gastraea_ form.

> It is clear that no stage in the present development is a typical gastrula stage, nor is there any stage which can be regarded as a specialized gastrula stage complicated by the formation of other organs; but a little study will show that the embryo presents at different periods all the phases in the formation of a gastrula, although there is no time when all the characteristics of a gastrula exist together. The gastrula _stage_ has disappeared, but the gastrula _form_ persists, and may be recognized by neglecting all those complications of structure which do not take part in its formation.[55]

Brooks, however, did not appear to doubt the fact that the prosobranch embryo shared a gastrula ancestry, for he attempted to explain how the _gastraea_ form could have become modified.

> If this [secondary modifications] were away, the embryo would then be a typical radically [sic] symmetrical gastrula. If the food yolk were wanting, the development of the wall of the digestive tract accelerated, the development of the foot, mouth invagination, velum and head vesicle retarded, we should have a true gastrula; or, conversely, the acceleration of the development of the latter organs, and the retardation of that of the digestive cavity, and the presence of a food yolk, might so modify a typical gastrula, as to give us the form of development which we find here.[56]

Additional work on other molluscs during the succeeding summer sessions of the CZL caused Brooks to adopt a far more reserved response to the universal gastrula. Although gastrula stages had been demonstrated in the embryonic life in all the groups of animals except Protozoa, Brooks doubted its status as an ancestral form.

> The gastrula theory cannot be regarded as one of the established generalizations of science, and the evidence which has so far been accumulated by embryologists is not by any means straight forward or satisfactory. The theory is one of the most interesting embryological problems under discussion, however, and any new information which bears upon it is of value.[57]

The information Brooks supplied to the gastrula theory dealt with the homology of the mouth, anus and primordial shell throughout Mollusca. All the evidence "furnished by Comparative Anatomy and Embryology" illustrated that these structures were homologous in all classes of the true Mollusca and were also homologous with the ancestral veliger form.[58] Brooks further noted that all the molluscan classes, based upon these homologies, could be represented at one time by a _proto_ _mollusc_. Since this prototypic form had to have appeared later in phyletic development than the _gastraea_ and, moreover, had to have been produced from the gastrula form, the mouth, anus and shell of the proto mollusc must bear some relation to the organs and openings of the ancestral Gastrae form. However, the blastopore of the gastrula, which according to Haeckel should exhibit homology throughout the Metazoa, bore no constant relationship in various molluscan embryos. In Paludina, the blastopore formed the anus; in Ostrea, the primitive mouth became the site of shell formation; and in Loligo the orifice had no connection with the mouth, anus or shell.[59] The results of the investigation opposed

> the conclusion that this stage has phylogenetic significance, and we are fully warranted in the statement that the present state of our knowledge forbids the acceptance of the gastrula theory as an established generalization of scientific value.[60]

Brooks did not, however, state that the evidence proved the gastrula theory to be completely erroneous, but only illustrated the lack of solid developmental evidence to support it.

> The general occurrence of a gastrula stage in so many widely separated animals is certainly the most pronounced feature in embryology, and it is possible that a more complete acquaintance with the development and phylogeny of the Mollusca may show that the facts held do not, in reality, oppose the view that it is in an ancestral form, and the conclusion which the facts seem to justify is not that the gastrula theory is proved or disproved, but that our acquaintance with the facts must be very much greater than at present before we shall be prepared to establish any general hypothesis as to the Metazoa.[61]

As previously mentioned, other morphologists had recognized various problems with the gastraea theory and had attempted to provide solutions to these problems through elaborations of the primitive condition. In the mollusca, W. Salensky had adopted E. Ray Lankester's planula theory to replace the ancestral gastrula form in *Ostrea*. However, Brooks demonstrated that a close examination of the early development clearly showed that a true invaginate-type gastrula stage appeared before the planula stage. Therefore, Brooks concluded the development of *Ostrea* was directly opposed to the "only consistent and probable hypotheses [Lankester's planula theory] which has been proposed in place of the gastrula theory."[62]

In other groups of animals, the planula theory appeared to fit the observations much better. Research on hydroid coelenterates showed that the segmenting egg developed into a ciliated planula stage. Brooks viewed this as probable evidence that the planula stage in the hydroids was the ancestral form and not the gastrula as was commonly accepted.

> I shall not enter upon the discussion of the relation of the embryology of the Hydromedusae to the gastrula theory, further than to point out that not a single hydroid gastrula has been observed; but that, in every species which has been studied, the digestive cavity has at first no opening to the exterior, and that the mouth is formed very much later than the stomach. Most writers believe, it is true, that the planula is a modified gastrula, and that its digestive cavity was originally invaginated from the exterior, but this is purely a deductive inference from the analogy of other animals.
>
> No one can question the resemblance between an adult hydroid or sponge, and the gastrula stage of the ordinary metazoa, and there is every reason for believing that the almost universal occurrence of this larval stage indicates that the coelomatous metazoa are the descendants of an ancestral form which was essentially like the existing coelenterates and that these themselves are the divergent modifications of a common type, the gastrula or two-layered metazoon, with stomach and mouth; but it is quite conceivable that the coelenterates themselves may be the descendants of a form with a stomach, but without a mouth, and that the planula stage may be the ontogenetic representative of this just as the gastrula stage is the ontogenetic representative of the adult coelenterate. Most writers have started however

> with the assumption that, as the hydroids must be the descendants of a gastrula, the planula must be a modified gastrula; and one writer has, with the greatest simplicity, given us the chain of reasoning which has led him to supply a missing gastrula stage in the life of the hydroids.[63]

Brooks suggested that the gastrula was not an universal developmental stage in all Metazoa. The hydromedusae provided evidence of a divergent branch represented by the planula larva.

> If we believe that the gastrula stage of the higher metazoa is the representative of an ancestral form like the adult hydroid, we certainly should not expect to find a gastrula stage in the embryology of the hydroids themselves; and the analogy of the animals above the hydroids is no reason for supposing that the planula is a modified gastrula if we believe that these forms are the descendants of an ancestral form which was itself a divergent branch from the coelenterate stem. The planula stage is certainly dominant among the sponges, and the so-called gastrula is here beyond a doubt a secondary larva.[64]

While Brooks could not support the Gastrae theory because it failed to hold up on close examination, he continued a research program that relied upon the closely related concept of homologous structures. Furthermore, he viewed the investigations of the gastrula theory as <u>the</u> fundamental morphological question.[65] After all, the entire phylogenetic aspect of morphology was premised upon the hypothesis that the germ layers throughout the Metazoa were homologous structures by virtue of their common descent from an ancestral form. But the necessary supporting evidence for the hypothesis was lacking or was not clearly articulated. Therefore, the acceptance of homologies based upon the ancestral <u>gastraea</u> was, at best, tentative.

> As long as the homology of the germ-layers and of the structures derived from them in the subordinate groups of

> Metazoa remains in uncertainty, any general hypothesis as to their homology throughout the entire Metazoa is clearly premature . . .[66]

In order to deal with questions of ancestral history, Brooks opted for determining homologies only within closely related groups. In his mollusc work, for example, he did not look for any evidence that would indicate the possible shared ancestry of the molluscs with other major phyletic groups. Instead, the diverse molluscan forms were studied in their developmental stages to determine, by the use of homologies, the ancestral mollusc condition. Brooks also denied the search for the ancestral *gastraea* form in each group. Evidence from the hydromedusae research indicated that this entire group of organisms lack a gastrula stage in development. Instead, Brooks looked to each group he was studying to determine the common ancestral form of that group. The result was that his phylogenetic work required much fewer large scale speculations and it relied more heavily upon developmental information. For example, Mollusca and Brachiopoda were represented by the veliger larval condition or by a *proto mollusc*, both of which could be demonstrated embryologically. The tunicates were traced back to an ancestor that resembled the present *Appendicularia* (or larval ascidian). Decapod crustaceans all shared a common nauplius stage. The planula represented the common ancestral form of the hydroids. To attempt to provide ancestral forms that were any more primitive involved one in too much speculative thought.[67]

By restricting his morphological research concerning phylogenetic history to ancestral forms within a restricted group, Brooks was not departing dramatically from arguments of common descent from a primitive gastrula form. Brooks, like Haeckel, was still attempting to determine the ancestral condition of a group of organisms. The real difference was in terms of scope and sophistication. By confining his work to a specific embryonic stage within a group of organisms, Brooks's phylogenies did not appear to be as speculative as those that traced all development to an ancestral _gastraea_. Furthermore, such a narrowing of scope was accompanied by an increasing attention to detail. Brooks's studies of hydroid ontogeny and phylogeny were impressive in terms of meticulous observation.

The narrowing of the scope of ancestral considerations also eliminated, or at least lessened, the problems with the concept of homology. From the _gastraea_, the morphologist was confornted with the problem of determining the homologies of both diploblastic and triploblastic structures from the same primitive ectoderm and endoderm. In Brooks's case, the homologies were traced back to the ancestral form of the group. For the molluscs, the primitive veliger stage contained a definitive mouth, anus, velum, shell gland, mantle and sensory tentacles that were homologous in all the molluscan classes. Brooks did not attempt to trace these structures back to a more primitive germinal layer for questions of phylogeny. Only in discussing issues of the individual's life history were considerations pre-dating the ancestral form considered.

Because of his own caution in discussing ancestral forms, it is not surprising that Brooks was very critical of any theory put forward by morphologists concerning the universal appearance of an ancestral form. His cautious rejection of Haeckel's gastrula theory and Lankester's planula theory have previously been cited. Brooks also opposed the viewpoint that all triploblastic organisms above the coelenterate (a transitional group) could be derived from a segmented ancestral form. This theory, championed by Adam Sedgwick and Anton Dohrn among others,[68] stated that Coelenterata and the triploblasts had a common origin from a coelenterate-like ancestor. The theory drew upon both Haeckel's and Lankester's viewpoint of a common ancestral form for all Metazoa.

> . . . all the most important organ systems of these Triploblastica are found in rudimentary condition in the Coelenterata; and that all the Triploblastica referred to must be traced back to a common diploblastic ancestor common to them and the Coelenterata.[69]

The segmented ancestor had its origin from the diploblastic ancestor as a result of an increased requirement for vegetative nutrition as the ancestral form increased in size. The result of these pressures was selection for an ancestral form with gut pouches. The pouches provided the origin point for the repeating somites which were characteristic of metazoans above the Coelenterata. Sedgwick's evidence for the hypothesis came from the similarity between the diploblastic state of Amphioxus development (pouched gut) and the polyp or medusa stage of selected hydroids (gut pouches).[70] Dohrn's elaboration of this theory traced the development of chordates back to an annelid ancestor. Again, the common characteristic was metameric body somites.

Brooks rejected the argument for the common origin of metamerism as indicating the existence of an ideal ancestor for Chordata, Arthropoda, Mollusca and Annelida because of its purely imaginary basis.[71] Brooks viewed the origin of the various tunicate structures as adaptations to biological conditions that prevailed in the pelagic ocean and not to the descent from an annelid-like ancestor. Even the segmented structures could be more accurately viewed as a gradual addition of successive complication to the tunicate structure.[72] Certainly this assumption was supported by studies of development and by knowledge of the habits of the tunicates.

> If the tunicates are, as their embryology and comparative anatomy indicate, the descendants of an ancestor which was obviously a free swimming animal, it is surely simpler, in view of all the facts, to regard the gill-slits as perforations which were originally retained and fixed by natural selection as channels for the exit of the water which was taken into the mouth with the food, than to refer them back to imaginary segmental organs which have left no other trace of their existence in the body of any known tunicata.
>
> Minute pelagic animals, with soft bodies bathed on all sides by pure water, do not need special organs of excretion or respiration, and it is not at all probable that the pharyngeal clefts were originally respiratory; but it is easy to understand how the channels through which the water flowed became converted into gill slits, in accordance with the law of change of function, as the descendants of the primitive tunicates grew larger and became sedentary, and thus came to need respiratory organs.[73]

Brooks had a similar criticism for ancestries of crustaceans that linked them to the segmented annelid. It was a common tendency to provide a phylogenetic explanation for duplicated structures. Therefore, since crustaceans exhibited metamerism were considered to have been derived from a metameric ancestral form. Brooks argued that vegetative duplication in one animal group did not necessarily indicate a phylogenetic link to a duplicated ancestor.[74] For Brooks, metamerism represented a case of general homology and could be traced to the common ontogenetic history that the duplicated parts shared. To understand the origin of metamerism in a group, the morphologist needed to examine the adaptations of the organisms to its biological conditions. It was reasonable, therefore, to see the phenomenon of metamerism in various taxonomic groups as a similar response to shared biological conditions and not as indicating a common phylogenetic origin. Such a viewpoint eliminated many problems in embryology in tracing the origin of somites in different animal groups.

Several of Brooks's critiques of various theories of ancestral phylogenies were due to his conviction that many morphologists did not utilize knowledge of the habits of organisms when constructing genealogies. Brooks stated that in his own work he sought to establish a direct connection between morphological studies and the facts of physiology and biology.[75] The monograph Genus Salpa provided a good example of Brooks's argumentation of morphological information and microscopical investigation with knowledge of the mode of life of Salpa. Brooks stated that these conditions for genealogical study were borrowed from Anton Dohrn.

> The homologies which are established by comparative anatomy, and the primitive identity which are established by

> comparative embryology are only the means for this end. They are in themselves valuable in phylogenetic inquiry only so far as they furnish us the opportunity to pass from the consideration of the structure of organs as they now exist, and of the functions of these organs at the present time, to the consideration of the conditions which have passed away; to the study of the history of the modifications which have come between these structures and functions and those which we must attribute to the same organs at an earlier genealogical stage.[76]

This type of careful analysis in genealogical work was characteristic of Genus Salpa and made it an example par excellence of late nineteenth-century morphology.

Brooks's work on the salps was not restricted to the morphology and genealogy of Salpa. A major interest in the morphological community was the establishment of a link between invertebrates and vertebrates. Such a connection had been suggested by Kowalewsky and was followed up by work of several investigators at Naples. Essentially all the major morphologists had commented upon the ancestry of vertebrates. At the conclusion of his Treatise on Comparative Embryology, F. M. Balfour stated the following.

> The present section of this work would not be complete without some attempt to reconstruct, from the materials recorded in the previous chapters, and from those supplied by comparative anatomy, the characters of the ancestors of the Chordata; and to trace as far as possible from what invertebrate stock this ancestor was derived.[77]

These reconstructions of vertebrate ancestry were certainly commonplace. Investigations of organisms that provided information for these genealogies became popular. Brooks recognized the value of work on Amphioxus in this regard.

> Amphioxus is a small worm-like animal, the lowest of the Vertebrates, and it is of great scientific interest since it has preserved many evidences of a relationship to various groups of invertebrates, and thus serves to bridge over the gap which was supposed by Cuvier and Agassiz to separate the Vertebrates from all lower forms of life. Its embryology which may be termed the key to the embryology of all the higher animals, has been ably studied by several of the most distinguished Zoologists of Europe, and a number of papers have appeared upon the subject within a few years.[78]

Like many of his peers, Brooks was keenly interested in vertebrate ancestry.

Brooks observations upon vertebrate ancestry were connected with his research on *Salpa*, as well as previous work both he and his students had conducted on *Amphioxus*, *Pyrosoma*, *Doliolum* and *Appendicularia*. His conclusions included the opinion that the vertebrate line of descent diverged early from a line of descent that included an early *Appendicularia*-like larval form, the solitary ascidians and the free tunicates.[79] *Salpa* had provided the developmental evidence that it passed through a larval form similar to *Appendicularia*, the solitary female *Salpa* indicated relationship to the sessile ascidians and the adult *Salpa*-chain represented the modern condition. However, even the larval condition indicated that the *Appendicularia* stage represented modifications that had taken place subsequent to the divergence of the vertebrate line. Therefore, while stating that the vertebrate line diverged from the line of development to the *Salpa*, Brooks did not speculate any further upon the character of the vertebrate ancestor.

Nevertheless, Brooks retained an interest in the development of Appendicularia due to its bearing upon vertebrate ancestry.

> Appendicularia is the modern representative of the tailed larva of Tunicates, and the oldest representative of the Vertebrate line, and its life history must be very instructive, but no one has found the eggs or young although the animal is found in all seas.[80]

Lacking the necessary life history information, Brooks examined the modern form and applied Dohrn's conditions for genealogical work; that is, he examined the structural conditions of the organisms in relation to its conditions of life to determine what functions might be attributed to the ancestral form. In this manner, he could speculate upon the path the modifications had traversed to the modern structure.[81] Brooks's conclusions were that the ancestor of Appendicularia was unsegmented, locomotor, pelagic and chordate-like. It had an unsegmented, axial notochord, an elongated and dorsal nervous system and a ventral digestive tube. The ancestral form did not have any pharyngeal gill clefts since the pharyngeal area was specialized for food gathering. The gill clefts were a later modification after specialization of the mouth.[82] All these characteristics were speculative and the acceptance of the ancestral form was provisional. As Brooks stated:

> . . . [one] cannot feel implicit confidence that the imaginary picture bears any minute and detailed resemblance to the actual history.[83]

Such a cautious approach characterized Brooks's contribution to the probable ancestral form of the vertebrate stock.[84]

Of major importance in considering Brooks's position vis-a-vis other morphologists was his tentative approach in the construction of genealogies. Brooks did not depart markedly from the use of speculation that was characteristic of the morphologist's search of ancestry. But he did restrict his speculative reconstructions to closely related animal forms. In this regard he departed from the common approach of attributing all metazoan descent from one ancestral form.[85] While his morphological studies implied the community of descent of all animal forms, Brooks found too many problems with the universal application of a single ancestral form. Observations from comparative anatomy and comparative embryology demonstrated the serious difficulties the morphologist had in determining the descent of all structures from the germinal tissue of the gastraea. A more accurate, meaningful and instructive approach was to study the homological relations of the animal forms belonging to one group.

Another problem that Brooks's restricted genealogies overcame was the observed fact that the paleontological record provided no evidence for the supposed divergence of the animal groups from each other. By the time fossil forms were preserved, the major groups of animals had become well established. Brooks used this point for his considerations of the ancestry of life. Since the morphologist had no direct evidence for the ancestry of the major groups, Brooks sought information in the developmental history of the organisms and in attention to the habits of life. He assumed that prior to fossilization there existed a rich pelagic stock from which the metazoans emerged.

> We may in the same way feel sure, even in the absence of sufficient evidence to trace their direct paths, that all the great groups of metazoa ran back to minute pelagic ancestors, and we must, therefore, include in the primitive pelagic fauna a great, but indefinite, number of distinct and somewhat widely separated ancestral forms, and together with them, no doubt, an equal or greater number of somewhat similar forms which have been exterminated and have left no descendants. In these extinct forms we should, if we could study them, find the connecting links between divergent groups, and we would thus be able to complete the genealogical tree of the metazoa by bringing together the great divergent branches of the metazoan stem whose primary relationships now seem beyond discovery.[86]

The ancestral forms present in the original pelagic fauna could be studied by the morphologists since evidence of the early life history was available.

> Biological evidence based on embryology and anatomy and on the habits and affinities of animals is justly regarded, by zoologists at least, as a more perfect record of the early history of life than paleontology, and we accept, without question, proofs of phylogeny which refer to a time very much more remote than the age of the oldest fossils.[87]

Using this method, which was characteristic of late nineteenth-century morphology, Brooks hoped to discover the divergence of the great metazoan groups.

The relationships of the metazoan groups were extremely difficult to elucidate since the primitive pelagic stock was so well adapted to the existing conditions. In fact, the pelagic conditions created a rather homeostatic environment for the existing marine life.

> Marine life is older than terrestrial life, and as all marine life has shaped itself in relation to the pelagic food-supply, this itself is the only form of life which is independent, and it must therefore be the oldest. There must have been a long period in primeval times during which there was a pelagic flora and fauna, rich beyond limit in

> individuals, but made up of only a few small simple types. During this time the pelagic ancestors of all the great groups of metazoa were slowly evolved, as well as others which have no living descendants. So long as life was restricted to the surface, no great or rapid advancement through the influences which now modify species was possible, and we know of no other influence which might have replaced these. We are, therefore, forced to believe that the differentiation and improvement of the primitive flora and fauna was slow, and that for a vast period of time life consisted of an innumerable multitude of pelagic organisms made up of a few forms. During the time which it took to form the thick beds of older sedimentary rocks the physical conditions of the ocean gradually took their present form, and during a part, at least, of this period, the total amount of life in the ocean may have been about as great as it is now without leaving any permanent record of its existence, for no rapid advancement took place until the advantages of a life on the bottom was discovered.[88]

Since there was little advantage to be gained by any new adaptation, the primitive fauna remained fairly static. Nevertheless, there had been enough change in time that the pelagic stock was not homogeneous, but contained all the ancestral forms of subsequent species. This hypothesis insured that evolution was not unidirectional, from a simple form to the more complex forms. Instead, there was no common direction in evolution since the pelagic forms already had developed along several distinct lines.

The surface of the ocean remained a suitable habitat for the simple fauna since these organisms were bathed in nutrients. Furthermore, the simple nature of the organisms was advantageous to this homogeneous environment. One additional factor that prohibited colonization of any other area than the pelagic dealt with the physical characteristics of the ocean. The benthos had little or no oxygen supply since this was totally consumed by the pelagics. As the flora built up slowly, this obstacle to colonization gradually eased as the plants built up the oxygen supply in the water. However, the shallow shoreline along the continental land masses, where the pelagics could have settled due to increased oxygen, was too sedimentary to provide a suitable habitat. The possibility of the invasion of a new environment by the pelagic life was presented by elevated areas in the sea far enough from the shoreline to be free of sediment and high enough from the benthos to insure an adequate supply of oxygen. Brooks held that it was here the first pelagic forms invaded the shallow water.[89]

The first settlers of the near-shore benthos did not benefit from more food sources, but the acquisition of nutrients was easier since food fell upon the organism from the pelagic region.[90] This allowed the initial colonizers to devote more energy for growth and multiplication, resulting in larger and more numerous forms. The sedentary life that was adopted became favorable for sexual and asexual multiplication which, in turn, led to rapid colonization and overcrowding of the bottom. Overcrowding placed selective pressures upon certain forms. The competition created rapid evolution in which the premium was upon the filling of every available habitat. The increase in the rate of evolution provided increased opportunities for divergent modifications. Increase in size led to an increased possibility of variation. Upon this variation natural selection operated to select the peculiarities which improved the efficiency of parts of the body in their functions in relation to each other. In this manner, Brooks explained the probable cause for the evolution of complicated organisms.[91]

From sedentary benthic forms certain organisms migrated secondarily back to the pelagic area. This was often the case for the larval forms since a move from the benthos could lessen competition for food and space. The secondary move brought about increased selection for new methods of protection, concealment and other advantages. This was the rationale for the secondary modifications of the larval forms of species that often occluded the ancestral type. With the maturation of the larva, the adult either returned to the benthic community or remained pelagic.

While much of Brooks's theory of the pelagic origin of the Metazoa was speculative, he attempted to provide supporting evidence for his views. He took great care to state that his statement on the primitive flora and fauna had nothing to bear upon the question of the beginning of life as this was "absolutely unknown at present."[92] His subsequent formulation of the flora and fauna was based on indirect evidence, or as Brooks maintained, his methods were "deductive" rather than "observational."[93] Nevertheless, there was ample material to support the hypothesis. For example, several marine groups had a uniform pelagic larval type.

> When all the members of a great group have a definite pelagic stage which adheres to the same plan of structure in all of them, we may be pretty confident that this larva is the representative of a primitive adult animal, even if this ancestor has now no unmodified descendants.[94]

The best example of such a primitive larval form was the nauplius larval stage for crustaceans. Other evidence came from modern pelagic adult animals. The minute size, simple structure and systematic affinity of *Appendicularia* and *Copepoda* revealed their primitive links to the former pelagic fauna.[95] These represented forms that became adapted to the pelagic zone while related species diverged to more advanced stages. Furthermore, it was typical of the present pelagic forms to be either descendants of benthic forms or larval stages of benthic forms that eventually settled when metamorphosing to the adult form.

All of these arguments were applied by Brooks in *Genus Salpa*. The salps provided excellent evidence for Brooks's theory. The larval form (*Appendicularia*) was pelagic. This gave rise to the sessile ascidian or the benthic-dwelling *Amphioxus*. Finally, budding from the sedentary form produced a third form, represented by *Salpa*, that was pelagic. Brooks considered the salps as mirroring the metazoan condition.

> Embryology also gives us good ground for believing that Salpa follows the analogy of all the metazoa in its still more remote descent from a small and simple pelagic ancestor, and there is good ground for believing that the earliest metazoa were all pelagic, and that they were represented at a very early period in the history of life by a floating or swimming animals of minute size and simple structure.[96]

Brooks's theory of the origin of the pelagic flora and fauna must be considered in terms of his position as a morphologist. Although a significant portion of the late nineteenth-century morphologists interpreted the ancestral-history aim of morphology as calling for elucidation of an universal ancestral form, Brooks rejected such a goal. Much of his early work pointed out deficiencies in such theories as the gastraea theory, the planula theory, the theory of segmental ancestors, etc. Instead, Brooks adopted a somewhat more restricted, but still speculative, goal of determining the common ancestral form of a specific group.[97] The desirability of such a research program becomes understandable when considered in light of Genus Salpa and the origin of pelagic life. Brooks maintained that existing evidence pointed only as far back in ancestral history as the condition in which all the major metazoan groups were established and well represented in the pelagic. Even at this point, Brooks stated, the evidence was often indirect and deductive. However, to attempt to trace ancestral forms back to an earlier stage involved the morphologist in insuperable difficulties. To minimize the speculative side of morphology, it was desirable to remain within the limits of evidence from paleontology, embryology, comparative anatomy and studies of the habits of organisms.[98]

2. Brooks as a defender of Darwin

The twin aims of the morphologist to study the form and structure of species and to elucidate the ancestral heritage of the species, directly involved the investigators in the question of the community of descent. Following the publication of the Origin of Species in 1859, there was, in essence, an universal acceptance of the theory of species descent.

> The great series of phenomena which could hitherto only receive a teleological explanation are thus brought into causal relation, and can be explained as the inevitable result of efficient causes, and their natural connection is thus rendered intelligible.[99]

Support for evolution came from the "whole of Morphology" which tended to show "the correctness of the theory of the transmutation of species."[100] Even the biogenetic law, which preceded the Origin of Species, became understandable in terms of the theory of descent.

> This parallel [biogenetic law], which naturally presents numerous greater or smaller variations in detail, is explained by the theory of evolution, according to which the developmental history of the individual appears to be a short and simplified repetition, or in a certain sense a recapitulation of the course of development of the species.[101]

Despite the several advantages of the theory and its widespread acceptance, there remained the need to explain the biological phenomena it described. To describe merely the community of descent was clearly inadequate.

> Practically, all scientists accept evolution as expressing a fact of nature. Having thus by their theory eliminated special creation of species, it becomes a logical necessity to show how the working of natural laws could have produced an evolution. To admit that the present species are descended from older ones is no advantage, unless it can be shown that new species can arise from old ones by the working of acknowledged laws of organic being. Two series of facts, it is plain, must furnish the data for all explanation: heredity and variation. By heredity, species reproduce their own kind; by variation, they produce offspring somewhat different from themselves. These two series of data are not theoretical, but actual. It is a universally recognized fact that animals and plants inherit from their parents, and it is also universally acknowledged that they vary very much. Out of these two series of facts, then, must the explanation arise.[102]

The reliance of evolution upon natural selection was widely criticized since selection theory offered only a physical explanation that had no bearing upon final causes. In short, natural selection proved the existence of a mechanical and causal connection between biological phenomena, but it had little to offer in terms of explaining the origin of the phenomena.[103] Several persistent questions continued to be asked of Darwinian evolution throughout the last quarter of the nineteenth century. How are characteristics inherited? What causes certain characteristics to vary? How are variations inherited? Is natural selection sufficient to account for the origin of adaptations or variations? In essence, there was a need to explain variation and heredity.

Darwin was aware of this weakness in his theory of descent. In an attempt to provide some basis for heredity and variation he developed a "provisional hypothesis" he called "Pangenesis."[104] The speculative theory was intended to provide a causal explanation for the phenomena included in the theory of descent.

> It is universally admitted that the cells or units of the body increase by self-division or proliferation, retaining the same nature, and that they ultimately become converted into the various tissues and substances of the body. But besides this means of increase I assume that the units throw off minute gemmules which are disposed throughout the whole system; that these, when supplied with proper nutriment, multiply by self-division, and are ultimately developed into units like those from which they were originally derived. These granules may be called gemmules. They are collected from all parts of the system to constitute the sexual elements, and their development in the next generation forms a new being; but they are likewise capable of transmission in a dormant state to future generations and may then be developed. Their development depends on their union with other partially developed or nascent cells which precede them

> in the regular course of growth. . . . Gemmules are supposed to be thrown off by every unit, not only during the adult state, but during each stage of development of every organism; but not necessarily during the continued existence of the same unit. Lastly, I assume that the gemmules in their dormant state have a mutual affinity for each other, leading to their aggregation into buds or into the sexual elements. Hence it is not the reproductive organs or buds which generate new organisms but the units of which each individual is composed. These assumptions constitute the provisional hypothesis which I have called Pangenesis.[105]

Darwin hoped that the pangenesis concept that called for each cell to give off individual gemmules would explain heredity and variation. According to this position, each fertilized egg contained gemmules representing all the cells of the parental generation. Hence, the inheritance of common traits was explained. At the same time, gemmules representing certain traits might remain dormant. This fact, along with the contribution of two complete sets of gemmules, would help to explain variation in the offspring.

Darwin's pangenesis hypothesis was generally not well received, although some of its implications were influential. The poor reception was due to several problems with the theory. First of all, if the gemmules were given off by every cell of an organism, the number of gemmules transferred to the sperm and the egg would be almost innumerable. Even if the gemmules were given a minute size, it was hard to understand how so many units of inheritance and variation could be packed into the germ cells. Second, while the character of the gemmules to be active at some times and dormant at other times explained variation in the offspring, it did not explain how organisms appeared to vary at the time in which change was needed. Additionally, it was difficult for Darwin's pangenesis view to explain why dramatic change, which would appear to demand that all the gemmules react in a given way, was sometimes on such a scale to effect whole tissue types, organs or structures. Third, the concept of fortuitous variation implicit in pangenesis could not explain why there was evidence of all individuals in a species exhibiting change in the same direction. These three examples illustrated some of the problems that the biological community had with Darwin's speculative view of the gemmules.

An even more damaging piece of evidence came from the research of Francis Galton (1822-1911). Galton conducted blood transfusion experiments on rabbits to determine the presence of the gemmules. The assumption behind the research was that the gemmules were carried within the blood. By transfusing the blood between distinct varieties of rabbits and then performing experimental matings, Galton attempted to determine the action of the gemmules. If they were carried in the blood, a transfusion of the blood from a different variety of rabbit into another rabbit should result in offspring, when the rabbits were mated, that had characters similar to the characters of the rabbit from which the transfused blood was taken. Even after repeated matings, all of Galton's experiments were negative. Therefore, Galton believed that the gemmules did not exist in the blood. Even Darwin was impressed with the work for he stated that he "certainly should have expected that gemmules would have been present in the blood . . . ."[106] However, Darwin held to the pangenesis hypothesis by stating that the work of Galton disproving the existence of the gemmules in the blood, did not disprove the whole theory since the gemmules were "no necessary part of the hypothesis. . . ."[107] Furthermore, he recognized the entire hypothesis as being provisional "until a better one be advanced. . . ."[108]

It may have been the provisional nature of the pangenesis concept or Darwin's call for a better theory than his speculative one that brought Brooks into the consideration of pangenesis. Certainly he was an adherent to Darwin's theory of descent and a vigorous supporter of various aspects of Darwinian evolution. In a letter to Ira Remsen written late in the nineteenth century, Brooks wrote of the importance of Darwin's work.

> In the more immediate subject of Biology, it is universally admitted that all the activity of the last thirty years owes its inspiration to his [Darwin's] work, and most of it follows lines which he marked out.[109]

Regardless of the exact nature of the impetus for Brooks's involvement with pangenesis, he became the best-known popularizer of pangenesis and the leading American neo-Darwinian in the late nineteenth century.

Brooks's original statement on pangenesis came in an address he gave to the American Association for the Advancement of Science (AAAS) meeting in Buffalo, New York on August 23, 1876.[110] The goal of the paper was to synthesize the hypotheses of Richard Owen (1804-1892), Herbert Spencer (1820-1903) and Charles Darwin, to retain all the valuable aspects of each, but to avoid the objections to each hypothesis. In his provisional view of pangenesis, Brooks theorized that the established characters of a species were transmitted through the ovum when it was properly stimulated.[111] New characters were transmitted via the gemmules, which were only given off by the cells involved in variation.[112] The gemmules themselves could not form new individuals, but under the proper conditions they could reproduce the cell that formed them. Since most cells were perfectly adapted to their surroundings, as a result of the evolutionary process, they did not give off gemmules. However, when an unfavorable state existed in the environment, it effected the prevailing adjustment between the cell and its environment. If the change was sufficient to effect the normal performance of the cell, gemmules were produced and transmitted via the germ cells to the next generation.[113]

Brooks's hypothesis also included a separate role for the male germinal tissue and female germinal tissue. The gemmules produced by the body were stored in the male gland, entered the seminal fluid and were transmitted to the egg by impregnation and fertilization. The ovary, on the other hand, lacked the specialized structures for the aggregation and transmission of gemmules. Therefore, while the cells of the female did produce gemmules, they were seldom important for the variation which was exhibited in the offspring.[114] The male, then, accounted for adaptations to environmental conditions, or was the original germinal element. The egg was the conservative material and accounted for the species' apparent adherence to the type.

Brooks's aim with his theory was to answer several of the major objections to Darwin's theory and to provide an hypothesis that would be supported by solid evidence. By stating that only cells undergoing variation produced gemmules, Brooks escaped the numerous difficulties of dealing with a vast multitude of gemmules. Moreover, Brooks felt this minimized the impact of Galton's experiments. If only a few gemmules were formed, it would be difficult to find them in the blood. Instead, they would tend to be localized in the male germinal tissue. Second, this view provided a simple explanation to why variations appeared when there was a need for the variations. Since gemmules were the cell's response to changed conditions, only when change occurred would they be produced. Third, the new conditions in the environment did not result in direct variation in that generation. Rather, as was observed, variations in response to change always appeared in the subsequent generation. Finally, by theorizing that the different germ cells had markedly different roles in heredity, Brooks appeared to provide a satisfactory solution to many observations. To cite one common example, in polymorphic species the male usually exhibited far greater variation than did the female. This was readily explained if the male was considered the variable parent while the female represented the conservative component.

The provisional hypothesis of Brooks was an attempt to provide a solution to the problem of the cause of heredity and variation, a secondary but nevertheless significant problem for morphology. With the revised theory of the gemmules and the differential role of the sperm and the egg, Brooks stated his solution. Each organism was the result of a dual influence; the law of heredity or the principle of adherence to the type, and the law of variation, or the principle of adaptation to conditions. The ovum provided the material medium for the law of heredity while the gemmule units of the sperm served as the means for variation or the law of adaptiveness.[115]

The most mature statement of Brooks on pangenesis came in 1883 when he published The Law of Heredity, his tour de force on questions of heredity and variation.[116] Brooks wrote at the outset that the work represented a modification of Darwin's pangenesis concept to meet the objections to Darwin's work and to clarify the theory, since the substance of the hypothesis was correct.[117]

> In a word, nearly all the phenomena of heredity admit of explanation by the hypothesis, and those who have criticized it have not usually attempted to show that it conflicts with fact, but have simply objected to it as a purely imaginary explanation.[118]

Brooks's own version of pangenesis in The Law of Heredity was essentially the same as developed in "A provisional hypothesis of pangenesis." His particular goal was to provide a law which would satisfy four objectives: one, to remodel pangenesis in order that only a few gemmules would be produced at any one time; two, to depict the gemmules as not necessarily being present at all times and in all parts of the body; three, to embrace a new class of facts in addition to the known functions of the sexual elements; four, to discover new and unexpected relations between phenomena.[119] Brooks considered his particular revision of pangenesis to accomplish all of these ends. The production of gemmules was related to the direct action of conditions surrounding a specific cell; change in one part of an organism could produce variation in a related part, therefore change often occurred when and where it was needed (not fortuitous); slight changes could produce dramatic variations; and similar changes in environmental conditions could cause analogous or parallel evolution among polyphyletic groups (a la Genus Salpa).[120] Using numerous examples of biological phenomena, many of which had been previously unexplained, Brooks demonstrated how his Law of Heredity was harmonious with observations from nature.

Another objective of Brooks was his desire to illustrate that his theory of heredity was supplementary to the theory of natural selection. The problem was, as Brooks saw it, that Darwin insisted the variations upon which natural selection acted to produce modification and adaptation were fortuitous. It was difficult to understand how such fortuitous changes could account for the observed facts of evolution, especially in the formation of complicated organs.

> Our theory of heredity furnished exactly what we need to escape this difficulty for we can understand that a change

> in any part of the body, disturbing, as it must, the harmonious adjustment of related parts, acts directly to produce variations in these parts in succeeding generations, by causing the transmission of gemmules. The time which is needed for the evolution of a complicated organ by natural selection is thus brought within reasonable limits and one of the most serious and fundamental objections to Darwin's explanation of the origin of species is completely done away with.[121]

Brooks expressed such coordinated modification of related parts as the action of correlated variability.[122] The correlation was a necessary cause of Brooks's own view of heredity; that is, it represented the response by the gemmules to changed conditions.

> According to our theory of heredity, when an organism, placed under new conditions, becomes modified to meet the change in its environment, the existence of the internal change is caused by the external change, while its precise character is determined by other factors, chiefly by the hereditary characteristics of the corresponding past, on both parents.[123]

The establishment of the law of heredity was due to the direct action of natural selection. It was natural selection that selected for cells to remain conservative during normal conditions and to throw off gemmules during conditions of change; natural selection led to the divergent specialization of the sexual elements; and natural selection created a physiological division of labor between the male and female elements.[124] In the higher organisms, the result of the action of natural selection was to create a situation in which it was subordinated to the law of heredity. However, Brooks was careful to insist that the subordinate status was secondary and was entirely due to the action of natural selection.[125]

Brooks's hypothesis on heredity and variation also represented a compromise between the two polar positions concerning evolution. Since inherited variations were not purely fortuitous (Darwin) or exclusively due to the direct modifying influences of the natural environment (Lamarck):

> The occurrence of a variation is due to the direct action of external conditions, but its precise character is not. . . .[126]
>
> Our theory furnishes us explanations which lie midway between Darwin's view of the origin of variation and the Lamarckian view, and thus enables us to escape both of these difficulties, for it shows us how the influence of changed conditions upon an organism may give rise to congenital variation in later generations, and it also shows us why variations tend to appear at the time and place where they are needed. It also shows how a considerable modification may appear suddenly and become hereditary.[127]

This was an important attempt at reconciling the two leading positions concerning evolution and the causes of heredity and variation. While the Darwinian theory of species descent was very popular and influentical following its publication, there was a resurgence of interest in neo-Lamarckian ideas that became marked in the 1870's and 1880's. The neo-Lamarckian position in America was closely associated with the publication of the <u>American Naturalist</u>, the large paleontological community, and with the written work of Alpheus Hyatt, E. S. Morse, A. S. Packard and E. D. Cope among others. The <u>Law of Heredity</u> was Brooks's overt attempt at incorporating the desirable aspects of both the neo-Darwinian position and the neo-Lamarckian view into a new synthetic approach to heredity and variation.

Alpheus Hyatt was among the first to respond to the Law of Heredity. In "Fossil Cephalopoda in the Museum of Comparative Zoology,"[128] published in 1883, Hyatt commented upon Brooks's work. Referring specifically to Brooks's distinction between the different roles of the two sexes, Hyatt noted:

> This theory has many notable facts in its favor, but it will be difficult to apply it in forms where there are but slight, or no distinctions between the sexes, and again to the lower branches of animals in some of which hermaphroditism is prevalent as it is among sponges and Protozoa.[129]

Hyatt stated that Brooks had mistaken a general result for a cause. Since the habits of a male were more varied than the habits of a female, it was not surprising that the male was more variable. Hyatt was also critical of the differential sex roles since sex differences were not apparent in the fossil forms (nautiloids and ammonoids) he had been studying. Moreover, Brooks had not included the works of E. D. Cope, J. A. Ryder, A. S. Packard or Hyatt on the subject of "quick evolution of forms."

> He [Brooks] also regards the fossils as very unreliable means of information in this respect, a point of view, which is founded upon time-honored prejudice, but where will the zoologist and embryologist get relations in time or any sufficiently extended information about the succession of forms, without a resort to fossils?[130]

Hyatt's critical appraisal of Brooks was aimed more in the direction of what Brooks's theory failed to do than in the direction of evaluating the merits of the view.

The review article in American Naturalist, a journal with a definite neo-Larmarckian bias, was far more receptive than was Hyatt.[131] The anonymous review included extensive excerpts from the Law of Heredity before offering an appraisal. Noting that Brooks's theory was open to many of the same objections as the theory of pangenesis, the reviewer interestingly suggested that a revision of Galton's experiment be applied to Brooks's new conception of the action of gemmules.[132] Nevertheless, the reaction was favorable.

> As a speculation it is a very neat one and the arguments and facts brought forward, most of them, however, from Darwin's works, will be read with interest. The theory is carefully thought out, well presented, and the work is a contribution of permanent value to a most difficult and elusive topic in philosophical biology. . . .
>
> Speculation in good hands has always been a fruitful source of discovery, and the simple endeavor to discover the laws of heredity may at least lead to fresh fields of research.[133]

Not surprisingly, the only strong reaction to the work was the failure of Brooks to present more data concerning the direct action of external conditions upon variation in organisms.[134]

One of the most extensive reviews of the Law of Heredity was written by Asa Gray (1810-1888), a leading American supporter of Darwin.[135] While Gray had reservations about Brooks's acceptance and modification of Darwin's speculative pangenesis view, he had high remarks concerning Brooks's qualifications for the project and his method of examination.

> An essay which aims to succeed where Darwin failed, to correct some of his judgments, to explain away difficulties in the theory of natural selection which he confessed his inability to meet, and especially which is to account for variation, which, if we remember rightly, Darwin thought unaccountable, is certainly a very ambitious undertaking. But the attempt is made with a full knowledge of the actual condition of the questions involved, and the case is argued with real ability by a naturalist who has already made a mark in investigation

> and shown aptitude in speculation. One sees the handiwork of a trained and accomplished zoologist, not of an amateur, who usually shows his want of mastery of the subject alike when he hits and when he misses the mark. As the author modestly has "little hope that [his] views will be permanently accepted in the form in which they are here presented" but yet may be expected "to incite and direct new experiments," and "thus ultimately help us to a clearer insight into the nature of the forces which have acted, and still act, to guide the evolution of life," a reviewer who has given his book a cursory examination may truly say that he shares equally his doubt and his expectations. For, when we come to his "new theory of heredity," we find that it is only a hypothetical modification of Darwin's hypothesis of pangenesis, an hypothesis in which Darwin himself seems to have taken little stock and to have had diminishing confidence. At which we need not wonder, the incongruity is so patent between the theory of natural selection, so happily based upon known causes and actual operations, and pangenesis, which invokes imaginary entities and endows them with just such qualities as may serve the occasion. The one stands on the solid ground; the other is in the air, and that of the thinnest. Yet is is not becoming nor safe to disparage hypotheses, for some that seemed to be tenuous are found to do real service. And that of Mr. Brooks has the great merit,--which he points out,--that it is capable of being tested by experiment, if not in animals, yet upon plants.[136]

Gray went on to describe the essential features of Brooks's theory of heredity, using many examples from Brooks to illustrate the theory. He stated that even though the theory may not explain all heredity phenomena, it did offer a substantial improvement to the ordinary pangenesis position.[137] Furthermore, Gray emphasized at several points in his review, that the "great merit" of the new theory was that it could be tested by experimentation. He was particularly impressed, as a botanist, by the opportunities for experiments upon plants to investigate the law of heredity. In spite of a few reservations concerning the pangenesis nature of Brooks's law, Gray was favorably disposed to the Law of Heredity.

The anonymous review in Science provided an interesting reception to Brooks's publication.[138] The article began as follows:

> Jaeger is quoted by Spencer as saying that there has been enough Darwinist philosophizing, and that it is now time to subject the numerous hypotheses to the test of investigation. While this is undoubtedly true, some hypotheses are necessary; and even incomplete and erroneous ones may be of great service by offering a series of definite problems for solution, instead of a class of facts. "An honest attempt to reason from the phenomena of nature can hardly fail to result in the discovery of some little truth." This is the keynote of the book before us, which is therefore worthy of very careful consideration, however unsatisfactory it may prove to be as an explanation of the great problems of heredity.[139]

The review then detailed the essential aspects of the Law of Heredity, noting the debt that Brooks had to Darwin. The reviewer objected to Brooks's reliance upon Darwin for support and to Brooks's uncritical acceptance and use of many unproven suppositions. The entire gemmule explanation was disputed, for example, since it was opposed to the current cell theory.[140] Despite the many criticisms, the review closed in praise of Brooks's work.

> But, in spite of all that has been said, Professor Brooks is entitled to the thanks of all students of biology for his clear statement of the problem, and the many suggestive fields for investigation here opened. The student of heredity will find in this book just what he needs to give him a clear conception of how the problem is to be attacked. The book is one of remarkable ability. The way in which apparently disconnected series of phenomena are brought together and shown to be special cases of one general principle, is indeed masterly. Even if every single proposition of the hypothesis is entirely untenable, Professor Brooks must always be credited with having made a most important step in advance. Assuming that the

> problem of heredity is at all capable of solution, some such clearing of the field is a necessity. If different observers will devote their energies to following up the various lines of inquiry which Professor Brooks has so ably suggested, we may be sure of most valuable and fruitful additions to our knowledge.[141]

Brooks's revision of pangenesis was also treated by many of the late nineteenth-century and early twentieth-century works investigating the problems of evolution, heredity and variation. H. W. Conn (1859-1917) in Evolution of Today,[142] saw the Law of Heredity as of possible importance in eliminating existing problems of heredity and variation.

> A more recent theory requires more extended notice, since it not only attempts to explain heredity, but also variation; and not only variation, but simultaneous variation affecting just those parts which need change. If this theory can expain [sic] the occurrence of numerous simultaneous changes in the organs which need change, and can demonstrate the inheritance of the effects of use, it is plain that a large portion of the difficulties which have arisen in the way of all theories are removed.[143]

Conn considered Brooks's view as a combination of Darwin's theory of pangenesis and the theory of Weismann.[144] The role of the female was to produce the material for heredity (Weismann). Variation was due to the action of gemmules (Darwin) that were collected in the sperm. However, variation only took place if the organism was not in harmony with its environment. In this manner, Conn stated that Brooks explained why variations usually appeared when they were needed.

> It is an important theory, because it is the first attempt to explain the origin of simultaneous variations for successive generations in those parts where change is needed. If it can be believed that these laws are real

> ones, it is plain that a long step is taken toward the solution of the problem of the modification of species. The various objections urged against natural selection, from the indefinitness and minuteness of the variations, all disappear. The views of those who believe in the great effect of use and disuse receive much support, and even the extraordinary births of Mivart are somewhat easily understood. This theory of heredity is therefore an addition to all the views we have examined.[145]

In his summary statement concerning the various theories of heredity, Conn considered Brooks's theory as highly synthetic. It allowed an explanation to natural selection for "the simultaneous variations which are necessary" and to the neo-Lamarckian view "by showing how the effects of use and disuse may be transmitted."[146] In other words, Brooks offered a synthesis of the Darwinian and Lamarckian positions in terms of heredity and variation.

> But, at the same time, this theory of Brooks, though valuable, is only an hypothesis, and many objections arise to prevent it from being accepted in its unmodified form.[147]

Like all other theories of heredity, Brooks's position was not, in Conn's opinion, proven.

August Weismann (1834-1914) included consideration of Brooks's ideas on heredity in his monographs. In Essay upon Heredity, Weismann noted:

> Furthermore, Brooks well-considered and brilliant attempt to modify the theory of Pangenesis, cannot escape the reproach that it is based upon possibilities, which one might certainly describe as improbabilities. But although I am of [the] opinion that the whole foundation of the theory of Pangenesis, however it may be modified, must be abandoned, I think, nevertheless, its author deserves great credit, and that its production has been one of those indirect roads along which science has been compelled to travel in order to arrive at the truth.[148]

Weismann considered Brooks's theory of heredity as the only view which agreed with his own on the production of variation through sexual reproduction. He disagreed, however, with Brooks's formulation of the gemmules since Weismann viewed this as a means to base a theory of the transmission of acquired characters. Weismann believed hereditary variability could only arise by direct changes in the germ plasm or by the mixture of germ plasms in fertilization.[149] He further disagreed with Brooks's conception of the dissimilar role of the sperm and egg in reproduction. Weismann felt the male and female had equal contributions to make to the developing egg.

> Brooks has with great ingenuity brought forward certain instances which cannot be explained without perfect confidence by Darwin's theory of sexual selection, but this hardly justifies us in considering the theory to be generally insufficient, and in having recourse to a theory of heredity which is as complicated as it is improbable. The whole idea of the passage of gemmules from the modified parts of the body into the germ cells is based upon the unproved assumption that acquired characters can be transmitted. The idea that the male germ-cell plays a different part from that of the female, in the construction of the embryo, seems to me to be untenable, especially because it conflicts with the simple observation that upon the whole human children inherit quite as much from the father as from the mother.[150]

Weismann repeated these objections to Brooks in a later work, The Germ Plasm.[151] His criticisms provide an indication of the extent to which Brooks's theory was known to the biological community.

In France, Brooks's theory was considered in the work of Yves Delage (1854-1920).[152] Delage provided an extensive summary of Brooks's "theories des germes femelles et des gemmules mâles," as a modification of Darwin.

> It appears, at first, that this modification of the Darwinian theory only complicates it and gives rise, with out advantages, to new objections. We will show that this is not so and that the new theory responds to all the objections and explains, better than the old theories, a mass of biological phenomena.[153]

Delage then dealt with Brooks's treatment of the objections to pangenesis and Brooks's explanation of "phénomènes biologiques" in terms of the Law of Heredity. In the critique of Brooks, Delage was far less charitable as he completely rejected Brooks's hypothesis.

> In order to simplify the theory of Darwin and to reconcile it with Galton's experiments, Brooks proposes two modifications: 1. diminish the female gemmules; 2. restrain the production of the gemmules in the male to cells undergoing variation.
>
> It is easy to demonstrate that these pretended simplifications simplify nothing; on the contrary they complicate the theory and cause more confusion, and they are in marked contradiction to the obvious facts.[154]

Delage followed this general criticism with specific problems concerning Brooks's theory of heredity. He concluded:

> If the theory of Darwin is not satisfactory, it is not changes of this type that will make it acceptable.[155]

John T. Gulick (1832-1913) referred to Brooks's hypothesis concerning the variability of the male and the fixity of the female in reference to environmental pressure.[156] He noted the suggestion that environmental pressure upon a species could place a selective advantage upon the production of males. This, as Brooks theorized, would increase the variability within the offspring, thus increasing the "plasticity" of the species.[157]

The role of the male element in variation and the female element in heredity that Brooks developed, was also stressed by J. Arthur Thomson (1861-1933) in Heredity.[158] Thomson provided a complete summary of Brooks's "valuable work entitled The Law of Heredity" as a modification of Darwin's pangenesis theory. Thomson concluded:

> The above theory, being important, has been stated at some length. Apart from the suggestion of variation as due to sexual intermingling, with which Weismann has made us more familiar--apart, too, from the suggestion of germinal continuity, the credit of which Brooks shares--there are several important points to be emphasized in the modification proposed. It is in unwonted and abnormal conditions that the cells of the body throw off gemmules. The male elements are the special centres of their accumulation; the female it is that keeps up the general resemblance between offspring and parent.[159]

Although Brooks's Law of Heredity was debated throughout the end of the nineteenth century and into the early part of the twentieth century, it appeared as if Brooks began to doubt the efficacy of his gemmule hypothesis after 1883. For example, for over ten years following the publication of Heredity, Brooks did not write anything substantial concerning his theory except for a few observations concerning the relative rates of variation in males and females.[160] In fact, the last reference to gemmules by Brooks was in a session of the Morphological Seminary in 1889. In the discussion, Brooks stated that essentially all variation was the result of sexual reproduction and, moreover, the entire object of sexual reproduction was to secure variation. Citing his agreement with Weismann, Brooks held that the germ plasm of the parent passed on to the offspring, thus explaining inheritance. Variation resulted from a combination of the germ plasms and the presence of gemmules. These gemmules were not acquired characteristics by the organism, but represented the response of specific cells to external conditions. The role of the gemmule was to carry a "predisposition" for change to the germ plasm.[161]

Subsequent sessions of the Morphological Seminary indicate Brooks completely dropped the concept of gemmules by 1893. In discussing heredity, Winterton Conway Curtis's (1875-1975) notes of the seminary indicated Brooks said the following:

> Whether or not every cell of the body contains potentially the structure of the whole species, the facts force us to believe this this [sic] is so of the germ cells; these latter contain potentially the structure of the species, and also the characters carried down from their ancestors; this does not mean that the original primitive germ at the beginning of all life contained potentially all that was to come after, altho' we might come around to this view.[162]

Thus it can be seen that Brooks still believed in germinal continuity and that his conception of heredity resided somewhere between preformation and epigenesis. To explain completely heredity, however, Brooks stressed that all the cells were under the influence of external influences. Stating his acceptance of ideas from Herbert Spencer, Brooks said:

> Life is not the activity of protoplasm but it is a <u>relation</u>, a relation existing between the organism and its external surrounding.[163]

There was no recourse to gemmules to explain the continuous adjustment between the internal and external states. Instead, Brooks followed Weismann by insisting that the continuity of the germ plasm was the only "tenable explanation of heredity."[164]

Brooks's position became slightly modified in 1895. He still maintained that inheritance was attributed to germinal continuity.

> I may take this occasion to say that I still regard inheritance as a corollary or outward expression of the continuity of living matter, although I am less confident than I was in 1883 of the importance of the distinction between somatic and germinal cells.[165]

However, Brooks maintained that reproduction did not create marked variation *a la* Weismann and Galton. For animals to breed together, they had to belong to the same species. Thus interbreeding species shared a common ancestry and, by implication, shared many of the same traits. Observations indicated, in fact, that two interbreeding parents differed only in terms of secondary characteristics.[166] As a result, variation was not to be found in the remote past history of the organism, but in the present. Brooks's statement on variation became a modification of the 1883 position; the occurrence of variation was due to the direct action of external characters but the character of the variation was controlled by internal factors.

> We now have positive evidence enough for each view to convince me that both are true; that every change which takes place in the organism from the beginning of segmentation to the end of life is called forth by some external stimulus either within the body or without; and yet that outcome of the whole process of development is what it is because it was all potential in the germ.[167]

Brooks was convinced that the position he took on inheritance was not a neo-Lamarckian hypothesis.[168] The question for the Lamarckian view was, could the Lamarckian factors produce even the incipient stages of adaptive modifications? Additionally,

> Is there any evidence that the influence of the environment is inherently beneficial? If there is no such evidence we must believe that all its effects, except the effects which are already deducible from adaptive structure, must be hap-hazard.[169]

In essence, Brooks believed there was no evidence that the Lamarckian factors could produce cumulative change that would result in adaptation. On the other hand, if natural selection selected for variation, it must result in adaptation.[170]

By 1904 Brooks completely dismissed the germ plasm theory. Instead, he stated that the species represented the result of the reciprocal interaction between the living being and the world around it, or as Charles Darwin stated, the "struggle for existence."[171] Brooks was reacting to the emergence of an old dispute in embryology that had resurfaced as the result of new directions of research.

> One of the fruits of this resolution was a wonderful series of observations and experiments upon the behavior of eggs and embryos under abnormal conditions, the results of which are so instructive, and so full of food for reflection, that they mark an epoch in the history of embryology, making one of its most notable chapters. In so far, the resolution to cease from arguing, and to get to work, has been altogether good, although one need read but little in the current literature of embryology to find that we have not succeeded in laying aside speculative questions. Many embryologists are now asking whether the cell-differentiation which takes place during individual development is inherent in eggs or in their chromatin, or

> induced by the interaction between the constituents of the egg, and between cell and cell, and between the developing embryo and the external world.[172]

Brooks felt that any investigation that separated the cell from the external environment in considering heredity was inadequate. One could not investigate only the germ plasm, the nuclear material or even the external environment.

> The doctrine that individual development is due to the reciprocal interaction between the embryo and its internal environment is inadequate, but when it is joined to the doctrine that ancestral development is due to the reciprocal interaction between the living being and its environment of competitors and enemies, it seems to me to give an outline of an epigenetic account of both individual development and ancestral development: an outline which it will require generations of investigators to expand and perfect. In view of this, is it not time to have done with the pre-Darwinian metaphysical notion of species as something that resides in living beings and is handed down by a substance of inheritance?[173]

Brooks's final statement upon heredity was printed in 1906. This formulation of inheritance was essentially the same as the views he published in 1904. The important character of the work was that, at this time, Brooks completely rejected the concept of pangenesis, there was no more consideration for gemmules and he did not mention the dissimilar role of the male and female germinal elements. Instead, all heredity and variation was explained in terms of the rather imprecise, but non-problematic, relation of the cell to its environment.

> According to this view, the species is not in the chromatin, nor in germ cells, nor in differentiated cells, nor in gemmules, nor in idioplasm, nor in biophore, nor in allelomorphs, nor in living beings at any stage of their existence, nor in the conditions of existence, because it is in that

> reciprocal interaction between the living being and the natural world, of which it is a part, which has been called the struggle for existence. Neither the stability of species nor the mutability of species is in living beings, because it is through extermination in the struggle for existence that the type is kept true to its kind, and also through this struggle that it becomes slowly changed.[174]

Brooks's statement that species formed epigenetically from the interaction between the living being and the environment can be considered as his attempt to create a unified plan for ontogeny and phylogeny. Following the tradition of Darwin, Brooks accepted the phylogenetic history of a species as resulting from natural selection and the struggle for survival. In 1906, Brooks used the same basis to construct a theory of ontogeny. Ontogenetic development was also a process that could be explained in terms of natural selection and the struggle for survival. In this manner, both the ancestral development and individual development of a species were the result of epigenesis. Since all developmental phenomena were to be explained in these terms, Brooks viewed both heredity and variation as "imperfect views of the facts."[175] That is, they were only appearances that resulted from the relationship that existed between the organism and its external environment.[176]

3. Evaluation: Brooks as a nineteenth-century morphologist

We have previously demonstrated that Brooks's research represented one of the aims of morphology: to provide descriptions of the form and structure of organic forms. It has been shown that Brooks interpreted this in terms of careful investigations concerning the details of the life history of hydroids, molluscs, crustaceans, tunicates, and brachiopods. The character of this aspect of his work was essentially the same as that of other morphologists. To evaluate Brooks as a morphologist, we must examine the effectiveness of this research in answering the major questions confronting morphology.

Basically all the major problems of morphological research had their origin in the quest of the morphologists to satisfy the second aim of their discipline: to elucidate the ancestral history of the species under investigation. Typical of most morphologists, Brooks relied heavily upon embryological studies for the reconstruction of phylogenies. Even though the embryological record provided indirect evidence of the past history of the organism (based upon the biogenetic law), Brooks considered this as far superior to the incomplete but direct evidence from paleontology and the largely inappropriate and indirect evidence from comparative anatomy.[177] To embryology he often appended observations concerning the subsequent life history and habitat of the organism. In some cases this evidence gave Brooks additional support upon which to advance a particular genealogical view.

Implicit in the morphologist's reconstruction of phylogenies was the acceptance of the doctrine of the community of species descent. Following the suggestions and/or investigations of Huxley, Darwin, Kowalewsky, Haeckel and others, investigators in the 1870's and 1880's assumed that their research would at some time point out an ancestral form common to all animal life. At the very least, a common metazoan was thought to be discoverable. Hypothetical ancestral forms (gastraea) were constructed, various theories were offered to explain the descent of higher forms from the common ancestral forms (metamerism, coelom theory) and the vertebrate theory of descent from an invertebrate form was developed. Perhaps the major problem behind this entire approach was that all these hypotheses were based upon the theory that through species descent all animals exhibited germinal continuity. That is, all the developmental stages of all organic beings could be traced to a primitive embryonic tissue. The morphologist had only to discover homological relationships between species to obtain information concerning the ancestral relationships. Homologies, it was generally accepted, resulted from common descent from a specific germ layer or specific region of the ancestral form. This complete foundation for genealogies became rather tenuous in the late 1870's and 1880's when an increasing amount of evidence indicated that the germ layer theory for homological structures was not universally correct. The problem became, upon what basis should phylogenies be constructed?

In the present chapter, we have examined in detail Brooks's response to phylogenies based upon common germ layers (his opposition to the gastraea theory) and his reformulation of a criterion for homologies. In Brooks's studies of various life histories, particularly involving molluscs, he noted that homologous structures (larval mouth and anus) of two species that were closely related could be derived from different germ layers or germ regions. Embryological observations of this nature caused him to be quite skeptical of any hypothesis that called for descent from one common ancestor. Instead, Brooks viewed the evidence as indicating that the major groups of animals could be traced back to a point in which they were all represented as distinct, differentiated larval forms.

> Most of the great types of animal life show by their embryology that they run back to simple and minute ancestors which lived at the surface of the ocean and that the common meeting point must be projected back to a still more remote time, before these ancestors had become differentiated from each other.[178]

As a result, as far as the morphologist could accurately trace the descent of a group based upon sound morphological evidence, was to the representative larval type of the group. Brooks proved tremendously effective in this regard. The hydromedusae shared a planula stage, the molluscs and brachiopods were both derived from a trochophore-like larva, the chordates evolved through a larval form that resembled Appendicularia and decapod crustaceans were represented in the primitive pelagic region by the nauplius larva.[179]

The restriction of morphological considerations only as far as a larval ancestor was employed as the criterion for homologies. Rather than to trace homologous structures back to a primitive germ layer, Brooks stopped with considerations from the larva. Obviously, theories of development, as a consequence, were also restricted within a specific group. On this basis, it becomes understandable why Brooks rejected universal theories of development.

> . . . it is necessary now only to remind readers that Dr. Brooks has come to the interesting conclusion that a simple pelagic form, of which Appendicularia is the nearest living representative, is the common ancestor of the Ascidians and the Chordates; and that consequently there can be only among such organs as are found in simple transparent, surface-living creatures any homologies between vertebrates and invertebrates; arguments linking annelids, crustacea, and so forth with vertebrates, because of similarities in segmentation, body-cavity, etc., are dismissed as empty shadows of morphological dreams.[180]

Brooks's reconstruction of phylogenies, as a result of the restriction to larval forms, were characterized by the amount of careful detail that supplemented the genealogies. Being necessarily speculative, they were nevertheless accurate in depicting probable pathways of descent. In addition, Brooks's work often resulted in correcting many previous speculative views that were based upon the consideration of only a few forms and ancestry to a common ancestor. A feature of the work he did was a careful consideration and evaluation of previous views on the ancestry of the group under discussion, a compilation of information bearing upon similar and related species and, finally, Brooks's meticulous studies of the life history of the organisms followed by a summary genealogy.

Additionally, Brooks did not accept the phylogenies as established fact. Recognizing the difference between knowledge based upon empirical observations and hypotheses founded upon deduction, he insisted that the speculative phylogenies were tentative, at best.

> If the naturalist is honest with himself, it seems to me that he cannot fail to come in time to hold his most cherished convictions subject to revision, and to value them only when they are verified by laying them alongside nature, and to regard absolute truth and necessary trust as meaningless words, because the beings of things is not absolute but relative to everything else in nature.[181]

Nevertheless, the speculations on genealogy represented an important aspect of morphology. They were instructive in that, being hypothetical, they could be used to initiate further research and investigation, to provide coherence to random observations, and to serve as points of debate.

This chapter has also investigated Brooks's contributions to the formulation of a theory of heredity and variation. In the Law of Heredity Brooks was successful in developing a theory that was a modification of Darwin's pangenesis view. In Brooks's mind, his goal was to remove the difficulties that Darwin's theory had encountered while retaining the gemmule concept and the continuity of germ plasm to explain the means by which variation and heredity took place. As a morphologist in the 1880's such a project was legitimate.[182] The problem was that Brooks retained the metaphysical gemmules. Therefore, many of the same criticisms that were leveled at Darwin, were also aimed in Brooks's direction. Nevertheless, the numerous book reviews of the Law of Heredity and treatment of Brooks's theory in the major monographs of heredity, revealed the impact of Brooks's work. While the reception to the theory was mixed, Brooks's elevation of important questions and problems for theories of heredity to explain, was widely recognized.

Brooks's final position concerning a theory of generation differed dramatically from the 1883 version. No doubt much of this difference was due to Brooks's expected poor reception, especially in terms of the ad hoc gemmules.[183] However, another aspect of the change was due to the fact that biological investigation was changing. In a related context, the expectations for theories of biological phenomena also changed. In the 1890's many investigations branched out from descriptive embryology in the morphology tradition. Instead of describing normal phenomena, these workers began to ask questions of the material upon which they worked in such a manner that by experimentation, they could obtain answers. Thus, new emerging sub-disciplines such as cytology and experimental embryology had little scientific use for hypothetical entities like gemmules. Furthermore, as these sub-disciplines of biology refined their techniques, research programs and strategies, it became clear to many workers that they were better equipped to answer specific questions. Many of these questions, such as heredity and variation, had been the subject of morphological debate for several decades. But the methods of morphology did not yield factual solutions to the questions.

The change in the nature of investigations following 1890 (particularly evident in the United States) will be a subject addressed in Chapter Five. It was also a subject upon which Brooks commented. Of interest in the following lengthy excerpt is the fact that, at the end of his career, Brooks saw the need for combining the two levels of development he had spent his career investigating. Although in the 1880's he referred to homological structures to indicate phylogenetic relationship and gemmules and germ plasms to explain ontogeny, in 1907 all biological phenomena were understandable only in terms of the relationship of the living organism to its environment.

> The gradual disappearance of attempts to invent evolutionary hypotheses to account for individual development, or ontogeny, and the return to a more epigenetic standpoint, based on experimental evidence that the ontogenetic development of eggs can be understood only through their reciprocal interactions with their internal and external environments, seem to me to be a notable reformation. It also seems to me that this reformation is only begun so long as we attribute to species, as contrasted with the individual, to the inherent potency of the germ.
>
> No theory of generation can be satisfactory unless it includes ancestral history as well as individual history, for phylogeny is a series of ontogenies. We cannot tolerate a dualistic biology, nor believe the species is in the egg, if its ontogeny is epigenetic. If the species is innate in a modern egg, it must have been innate in the preceding egg, and so on back to the beginning, and we are entangled once more in the chains of the preformationists, from which the epigenetic view of ontogeny professes to set us free.
>
> I believe we have a simple and obvious path out of this paradox in the fact that the kinship and the individuality of a living being are inseparable; that heredity and variation are not facts, but imperfect views of the facts.
>
> I am a firm believer in the possibility of tracing the wider kinship of living things through their embryology. I am thoroughly convinced that ontogeny helps us to study ancestral history as I am convinced that paleontology helps us. In my opinion, there is a good foundation for the recapitulation theory, even if this foundation be too weak to hold up all the phylogenetic trees that have been planted on it.[184]

At the end of his career, therefore, Brooks reverted to an explanation for generation that had no final cause, essentially the same problem that faced the morphologist following Darwin. However, the aim of morphology to study the ancestral history through the developmental record remained a viable method of investigation.

NOTES

CHAPTER FOUR

1. T. H. Huxley, "On the Anatomy and Affinities of the Family of the Medusae," Philosophical Transactions of the Royal Society of London (1849), pp. 413-434.

2. Charles Darwin, On the Origin of Species, ed. by Ernst Mayr (Facs. 1st ed., Cambridge, Mass.: Harvard University Press, 1964).

3. H. V. Wilson, trans., "Metschinkoff on Germ Layers," American Naturalist 21 (1887), pp. 334-350, 419-433.

4. Haeckel continued to refine his position throughout the 1870's to meet new observations. The English-speaking community (especially important for the United States) received these modifications in the form of several translations. These included Ernst Haeckel, "The Gastraea-theory, the Phylogenetic Classification of the Animal Kingdom and the Homology of the Germ-Lamellae," Quarterly Journal of Microscopical Science 14 (1874), pp. 142-164, 223-235; Ernst Haeckel, The Evolution of Man (Akron, Ohio: The Werner Company, 1876); Ernst Haeckel, The History of Creation, trans. by Miss L. D. Schmitz, 2 vols. (New York: D. Appleton and Company, 1872).

5. Patrick Geddes, "Morphology," Encyclopaedia Britannica, 9th ed., 1883, Vol. 16, p. 840.

6. Ibid., p. 845.

7. Carl Gegenbaur, Elements of Comparative Anatomy, trans. by F. Jeffrey Bell (London: Macmillan and Company, 1875), p. 36.

8. Ibid., p. 63.

9. E. Ray Lankester, "Notes on the Embryology and Classification of the Animal Kingdom: Comprising a Revision of Speculations Relative to the Origin and Significance of the Germ Layers," Quarterly Journal of Microscopical Science 17 (1877), pp. 399-454.

10. F. M. Balfour, A Treatise on Comparative Embryology, 2 vols., (London: Macmillan and Co., 1880). This work was used by Brooks throughout the end of the nineteenth century.

11. Ibid., Vol. I, pp. 4-5.

12. Ibid., p. 479.

13. Ibid., p. 276.

14. Ibid., p. 283.

15. Ibid., p. 317.

16. Ibid., p. 284.

17. Adam Sedgwick, "On the Origin of Metameric Segmentation and Some Other Morphological Questions," Quarterly Journal of Microscopical Science 24 (1884), pp. 43-82.

18. Ibid., p. 68.

19. Ibid., p. 59-60.

20. Ibid., p. 69.

21. Carl Claus, Elementary Textbook of Zoology, trans. by Adam Sedgwick (4th edition, London: Swan Sonnenschein & Co., 1892).

22. Ibid., p. 118.

23. Ibid., p. 122.

24. Ibid., p. 146.

25. Ibid., p. 151.

26. Ibid., p. 159.

27. H. V. Wilson, trans., "Metschnikoff on Germ Layers." Wilson's translation was taken from Elias Metchinkoff, Embryologische Studien an Medusen (Wien, 1886). Many other important morphological papers and treatises that were published in foreign languages with limited circulation became available to the American community through the translation efforts of Brooks and his students.

28. Ibid., p. 338.

29. Ibid., pp. 420, 427.

30. Ibid., p. 431.

31. Arnold Lang, Textbook of Comparative Anatomy, trans. by H. M. and Matilda Bernard (London: Macmillan & Co., 1891). Originally the book was published as Lehrbuch der Vergleichenden Anatomie Uber der Werbellosen Thiere (Jena: Fischer, 1884-1894). The German edition was included on Brooks's reading list for graduate students in 1890. Appended to the list was a note that the work was still in publication. The English edition was available in 1891.

32. Ibid., pp. 55-57.

33. Carl Gegenbaur, Elements of Comparative Anatomy, pp. vii-viii.

34. W. A. Herdman, "Report upon the Tunicata Collected during the Voyage of the HMS Challenger during the Years 1873-1876," Report on the Scientific Results of the Voyage of the HMS Challenger during the years 1873-1876 - Zoology 27 (London: Eyre & Spottiswoode, 1888), p. 1-165.

35. C. O. Whitman, "A Contribution to the History of the Germ-Layers in Clepsine," Journal of Morphology 1 (1887), p. 107.

36. Edmund B. Wilson, "The Embryology of the Earthworm," Journal of Morphology 3 (1889), pp. 388-450.

37. Ibid., p. 428.

38. Ibid., pp. 441-442.

39. "Morphological Seminary, December 9, 1889 - Notes," Princeton University, Firestone Library Manuscript Room, E. G. Conklin Papers.

40. The various echinoderm classes, an example Brooks frequently used, were already well formed by the time they appeared in the fossil record. Therefore, stem forms of the echinoderm were lacking. It was this information that the morphologist needed to determine the exact phylogeny.

41. "Morphological Seminary, December 5, 1893 - Notes," University of Missouri, Elmer Ellis Library, Western Historical Manuscript Collection, Winterton Conway Curtis Papers.

42. W. K. Brooks, "Speculative Zoology," Popular Science Monthly 22 (1882), p. 203.

43. W. K. Brooks, "The Affinity of the Mollusca and Molluscoida," Proceedings of the Boston Society of Natural History 18 (1876), p. 234.

44. "General Zoology Notebook - JHU, November 8, 1888," E. G. Conklin Papers, Princeton University, Firestone Library Manuscript Room.

45. W. K. Brooks, "Speculative Zoology," p. 369.

46. Ibid., p. 374.

47. Ibid., p. 377.

48. W. K. Brooks, "The Development of Salpa," Bulletin of the Museum of Comparative Zoology 3 (1876), p. 339.

49. W. A. Herdman, "Report on the Tunicata," p. 121.

50. W. K. Brooks, "Salpa and its Relation to the Evolution of Life," Johns Hopkins University, Studies from the Biological Laboratory 5 (1893), p. 156.

51. W. K. Brooks, The Law of Heredity. A Study of the Cause of Variation, and the Origin of Living Organisms, (Baltimore: J. Murray, 1883), p. 309.

52. Ibid., p. 308.

53. W. K. Brooks, "The Homology of Cephalopod Siphon and Arms," American Journal of Science 20 (1880), pp. 288-291.

54. "Morphological Seminary - 11th lecture, December 5, 1893," University of Missouri, Elmer Ellis Library, Western Historical Manuscript Collection, Winterton Conway Curtis Papers.

55. W. K. Brooks, "Preliminary Observations upon the Development of the Marine Prosobranchiate Gasteropods," Johns Hopkins University, Studies from the Biological Laboratory 1 (1878), p. 13.

56. Ibid., p. 13.

57. W. K. Brooks, "Development of the American Oyster," Johns Hopkins University, Studies from the Biological Laboratory 1 (1880), p. 23.

58. Ibid., p. 76.

59. Ibid., p. 75.

60. Ibid., p. 76.

61. _Ibid_., p. 77.

62. _Ibid_., pp. 72-74.

63. W. K. Brooks, "The Life History of the Hydromedusae," _Memoirs of the Boston Society of Natural History 3_ (1886), p. 401.

64. _Ibid_., p. 402.

65. W. K. Brooks, "Observations upon the Early Stages in the Development of the Fresh-Water Pumlonates," _Johns Hopkins University, Studies from the Biological Laboratory 1_ (1879), p. 73.

66. W. K. Brooks, "The Development of the Digestive Tract in Molluscs," _Proceedings of the Boston Society of Natural History 20_ (1879), p. 325.

67. Brooks, however, did trace the various larval forms to a more remote ancestral condition. In _The Genus Salpa_, he included a discussion of the evolution of the pelagic fauna in which this topic was expounded upon. This will be discussed at a later point in this chapter.

68. Adam Sedgwick, "On the Origin of Metameric Segmentation," and Anton Dohrn, _Der Ursprung der Wirbelthiere und das Princip das Funtionswechsels. Genealogische Skizzen_ (Leipzig, 1875). Both works were included on Brooks's reading list for graduate students in 1890.

69. Adam Sedgwick, "On the Origin of Metameric Segmentation," p. 68.

70. _Ibid_., p. 58.

71. W. K. Brooks, _The Genus Salpa. Memoirs from the Biological Laboratory of Johns Hopkins University 2_ (Baltimore: The Johns Hopkins University Press, 1893).

72. _Ibid_., p. 188.

73. _Ibid_., pp. 194-195.

74. _Ibid_., p. 162.

75. _Ibid_., p. 178.

76. _Ibid_.

77. F. M. Balfour, Treatise on Comparative Embryology, Vol. II, p. 258.

78. "Chesapeake Zoological Laboratory," Johns Hopkins University Presidents Report (1878).

79. W. K. Brooks, The Genus Salpa, pp. 138-139.

80. Letter, W. K. Brooks to D. C. Gilman, May 4, 1894, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman Collection.

81. W. K. Brooks, The Genus Salpa, p. 178.

82. Ibid., pp. 179-180.

83. Ibid., p. 184.

84. O. Seeliger, "Review of The Genus Salpa," Zoologische Zentralblatt 1 (1894), pp. 900-908.

85. This same trend became a marked characteristic of Brooks's students.

86. W. K. Brooks, The Genus Salpa, p. 159.

87. Ibid., p. 166.

88. Ibid., pp. 167-168.

89. Brooks's viewpoint on the development of elevated areas was supported by the paleontological and geological work of Charles Doolittle Walcott (1850-1927). Brooks extensively utilized Walcott's work.

90. W. K. Brooks, The Genus Salpa, p. 169.

91. Ibid., pp. 170-173.

92. W. K. Brooks, "Salpa in its Relation . . .," p. 148.

93. Ibid., p. 148.

94. Ibid., p. 149.

95. Ibid., p. 150

96. Ibid., p. 144.

97. This particular method is frequently used by invertebrate zoologists and embryologists to classify each group of

organisms to a common type.

98. O. Seeliger, "Review of The Genus Salpa" and "Book Review - The Genus Salpa," Popular Science Monthly 45 (1894), pp. 272-273.

99. Carl Claus, Elementary Textbook of Zoology, p. 146.

100. Ibid., p. 151.

101. Ibid., p. 159.

102. H. W. Conn, Evolution of Today (New York and London: G. P. Putnam's Sons, 1889), p. 283.

103. Carl Claus, Elementary Textbook of Zoology, p. 147.

104. Charles Darwin, The Variation of Animals and Plants Under Domestication, 2 Vols. (London: John Murray, 1868).

105. Ibid., pp. 369-370.

106. Ibid., p. 350.

107. Ibid.

108. Ibid.

109. Letter, W. K. Brooks to Ira Remson, January 30 [n.d.], Johns Hopkins University, Eisenhower Library Manuscript Room, Remsen Collection.

110. W. K. Brooks, "A Provisional Hypothesis of Pangenesis," American Naturalist 11 (1877), pp. 144-147.

111. This represents one of the initial remarks concerning germinal continuity. It was noted by August Weismann, who became identified with the theory of germinal continuity.

112. Ibid., p. 144.

113. Ibid., p. 146.

114. Ibid., p. 145.

115. W. K. Brooks, "The Condition of Women from a Zoölogical Point of View," Popular Science Monthly 15 (1879), pp. 146, 150.

116. W. K. Brooks, The Law of Heredity.

117. In considering the objections to pangenesis, Brooks undertook a survey of essentially all the investigators, European and American, working upon questions of heredity. The Law of Heredity represents, in this regard, a valuable commentary upon the state of heredity concepts circa 1883.

118. W. K. Brooks, The Law of Heredity, p. 51.

119. Ibid., pp. 80-81.

120. Ibid., p. 328.

121. Ibid., p. 287.

122. Ibid., p. 291.

123. Ibid., pp. 292-293.

124. Ibid., p. 294.

125. Ibid., p. 294.

126. Ibid., p. 83.

127. Ibid., p. 164.

128. Alpheus Hyatt, "Fossil Cephalopoda in the Museum of Comparative Zoology," Proceedings of the American Association for the Advancement of Science 32 (1883), pp. 347-348.

129. Ibid., p. 348. Hyatt may have been overstating this criticism since Brooks maintained his theory applied most effectively to higher, multicellular animals.

130. Ibid.

131. "Recent Literature: Brooks' Law of Heredity," American Naturalist 17 (1883), pp. 1262-1265.

132. Ibid., p. 1264. The suggestion was: "To test the theory properly we should think experiments might be made by inoculating with the supposed gemmules the testes of different mollusks or other low animals [not an unusual suggestion since it was made by paleontologists who worked almost exclusively on these forms]; but none have been reported by the author.

133. Ibid.

134. This criticism was quite inappropriate. Brooks's Law of Heredity was an attempt to explain the role of environmental

influences upon variation. The theory definitely states that the action of the environment was not direct; rather, it acted through the influence of the gemmules.

135. Asa Gray, "Book Notices," review of The Law of Heredity, by W. K. Brooks, in Andover Review 1 (1884), pp. 208-214.

136. Ibid., p. 210.

137. Ibid., p. 212.

138. "A New Theory of Heredity," review of The Law of Heredity, W. K. Brooks, in Science 3 (1884), pp. 388-390.

139. Ibid., p. 388.

140. Cells only arose from pre-existing cells, not spontaneously as would probably be the case in gemmule propagation. The known phenomena associated with impregnation also were at odds with the gemmule concept. The sperm appeared to coalesce with the egg and no yolk was lost. The action upon the egg was apparently of equal modifying action.

141. Ibid., p. 390.

142. H. W. Conn, Evolution of Today.

143. Ibid., p. 277.

144. Like Weismann, Brooks stressed (independently) the germinal continuity between generations through the material of the ovum. Heredity was due, on this view, to descent from the same ovum.

145. Ibid., pp. 281-288.

146. Ibid., p. 286.

147. Ibid., p. 286.

148. August Weismann, Essays upon Heredity and Kindred Biological Problems, edited by Poulton, Schönland and Shipley (Oxford: Clarendon Press, 1889), p. 166.

149. Ibid., p. 327.

150. Ibid., p. 332.

151. August Weismann, The Germ-plasm: A Theory of Heredity (London: Walter Scott, Ltd., 1893), pp. 412-413.

152. Yves Delage, La structure du protoplasma et les théories sur l'hérédité et les grands problèmes de la biologie générele (Paris: C. Reinwald, 1895).

153. Ibid., p. 605.

> Il semble, au premier abord, que cette modification à la théorie darwinienne ne fasse que la compliquer et donne prise, sans advantage, à des objections nouvelles. Nous allons montrer qu'il n'en est pas ainsi et que la théorie novelle répond à toutes les objections et explique, mieux que l'ancienne, une foule de phénomènes biologiques jus qu'ici inexpliqués.

154. Ibid., pp. 613-614.

> Pour simplifier la théorie de DARWIN et la concilier avec les expériences de GALTON (71), BROOKS propose deux modifications: 1° subprimer les gemmules chez la femelle: 2° restrendre leur production chez le mâle aux moments où les cellules varient.
>
> Il est facile de montrer que ces prétendues simplifications ne simplifient rien; qu'elles compliquent, au contraire, la conception et la rendent très confuse, et qu'elles sont en contradiction flagrante avec des faits indiscutables.

155. Ibid.

> Si la théorie de DARWIN n'est pas satisfaisante, ce n'est pas par des variantes dans le genre de celle-là gu'on la rendra acceptable.

156. John T. Bulick, Evolution. Racial and Habitudonal (Washington, D. C.: Carnegie Institution of Washington, 1905).

157. Ibid., p. 190.

158. J. Arthur Thomson, Heredity (New York, London: G. P. Putnam's Sons, John Murray, 1907).

159. Ibid., p. 410. A similar appraisal of Brooks was contained in another work by Thomson: Patrick Geddes and J. Arthur Thomson, The Evolution of Sex (New York: Charles Scribner's Sons, 1907), pp. 11-13.

160. The major publication by Brooks was "Influences Determining Sex," Popular Science Monthly 26 (1885), pp. 323-330. Other smaller articles contained the same observations as this article.

161. "Morphological Seminary - Notes, October 15, 22, 29, 1889," Princeton University, Firestone Library Manuscript Room, E. G. Conklin Papers.

162. "Morphological Seminary - Notes, March 9, 1893," University of Missouri, Elmer Ellis Library, Western Historical Manuscript Collection. Winterton Conway Curtis Papers.

163. Ibid.

164. Ibid.

165. W. K. Brooks, "An Inherent Error in the Views of Galton and Weismann on Variation," Science 1 (1895), pp. 121-126.

166. Ibid., p. 124.

167. Ibid., p. 125.

168. Brooks published a series of rebuttals to this charge first leveled by George Romanes in reference to The Law of Heredity. The articles disputing the charge include: W. K. Brooks, "Lamarck and Lyell: A Short Way with Lamarckians," Natural Science 8 (1896), pp. 89-93; W. K. Brooks, "Lyell," Johns Hopkins University, Circulars 15 (1896), pp. 78-79; W. K. Brooks, "Lyell and Lamarck: A Consideration for Lamarckians," Johns Hopkins University, Circulars 15 (1896), pp. 77-78; W. K. Brooks, "Lyell and Lamarckism: A Rejoinder," Natural Science 9 (1896), pp. 115-119.

169. W. K. Brooks, "Lamarck and Lyell," p. 91.

170. Ibid., p. 92.

171. W. K. Brooks, "Individual Development and Ancestral Development," in Congress of Arts and Science 5 (St. Louis, 1904), p. 314.

172. Ibid., p. 308.

173. Ibid., p. 319.

174. W. K. Brooks, "Heredity and Variation: Logical and Biological," Proceedings of the American Philosophical Society 45 (1906), p. 75.

175. W. K. Brooks, "Are Heredity and Variation Facts?" Advance print from Seventh International Zoological Congress, Boston Meeting, August 19-24, 1907.

176. "The Seventh International Zoological Congress," Nature 76 (1907), pp. 471-473. The article represents a long summary of the entire Congress. Of interest was the fact that of all the papers delivered at the Congress, the author of the article singled out two to deal with in some length. The first was Jacques Loeb's work on the chemical character of fertility. The second was Brooks's paper, "Are Heredity and Variation Facts?" The summary was very favorable to Brooks, quite extensive and referred to Brooks as the "genial iconoclast."

177. W. K. Brooks, Foundations of Zoology, p. 220.

178. Ibid., p. 217.

179. Of interest is that it is a common feature of contemporary invertebrate studies to group organisms from a common larval type. In many cases Brooks's larval forms are still accepted (Hydromedusae work).

180. "Some New Books, The Monograph on Salps," review of The Genus Salpa, by W. K. Brooks, in Natural Science 4 (1894), p. 462.

181. W. K. Brooks, "The Intellectual Conditions for the Science of Embryology," Science 15 (1902), p. 491.

182. This thrust of Brooks's work was secondary to the strict application of morphological research.

183. Brooks wrote: "My book found the oblivion which it no doubt deserved . . . ." (W. K. Brooks, "Lamarck and Lyell," p. 91).

184. W. K. Brooks, "Are Heredity and Variation Facts?", p. 42.

Chapter Five: Morphology and the Emergence of Experimental Biology in America

In the last year of the nineteenth century, William Keith Brooks delivered a series of lectures at Columbia University that were subsequently published in book form.[1] The subjects of the lectures touched on the most fundamental issues of nineteenth-century biology. These subjects were treated in such a manner that they illustrated Brooks's central position in biology. David Starr Jordan, then president of Stanford University and an old acquaintance of Brooks, made the following comments upon Foundations of Zoology, the published form of the lectures, in a feature review in Science.

> The stones which Dr. Brooks has chosen as "Foundations of Zoology" will remain there for centuries, most of them as long as human wisdom shall endure. The volume is a permanent contribution to human knowledge, the worthy crown of a life of wise thought as well as of hard work and patient investigation. . . .
>
> The biologists of America have long since recognized Dr. Brooks as a master, and this volume, the modern and scientific sequel to Agassiz's "Essay on Classification" places him in the line of succession from the great interpreter of nature, whose pupil and friend he was.[2]

The "line of succession" Jordan referred to can be legitimately applied to the development of American morphology. At the end of the nineteenth century, Brooks epitomized the methods and goals of morphological research. In Foundations of Zoology, he noted the maturation of this aspect of biological work.

> During the last half-century natural science has become historical. We have opened and learned to read a new chapter in the records of the past. The attributes of

> living things, which seem to the older naturalists to be complete and independent in themselves, have proved to have a history which can be studied by the methods of science. They have been found to be steps in a long sequence of events as orderly and discoverable as the events which are studied by the astronomer or the geologist.[3]

By the early 1890's, American morphology had definitely matured into a well-defined discipline complete with its own journal. In 1887, the Journal of Morphology was established, with C. O. Whitman serving as editor.[4] As a result, the majority of the articles published between 1887-1910 were of a descriptive nature, based upon observations of biological phenomena. The descriptive character also mirrored the twin goals of morphology; that is, it was primarily concerned with the form and structure of organisms and the bearing that the form of the organism had upon its ancestral heritage. Like morphology of the earlier period, studies in the early 1890's emphasized descriptive investigations of the early developmental stages. It was precisely these embryological observations that had the most bearing upon questions of ancestry. The Journal of Morphology was not alone in illustrating this character of American science. Perusals of Science, American Naturalist and Proceedings of the Boston Society of Natural History also reveal that a major concern of the American biological community was directed toward morphological studies, particularly those involving development. This generalization applies accurately through to the end of the nineteenth century.

Morphological studies also utilized, as we have seen, evidence from comparative anatomy and paleontology. However, both of these methods of investigation were fraught with problems that caused them to have minimal impact on the studies. Consequently, embryological work, the third approach in morphology, predominated. Its application to questions of ancestry in its descriptive form was well known.

> There are, indeed, two methods by which embryology, like any other branch of zoology, may be investigated. One is purely descriptive, anatomical, morphological. By this method, truly, great results have been achieved. The life-histories of members of all the most important groups of the animal kingdom have been worked out, and the science of Comparative Embryology has been built up. Nor has an explanation of the process been lacking. For ontogeny is, the fundamental Biogenetic Law assures us, a recapitulation of and therefore explicable in terms of phylogeny; and since on this principle the individual repeats in its development the ancestry of its race, embryology affords a means of tracing out the relationships of the organism and establishing the homologies of its parts.[6]

Unfortunately, as early as the 1880's morphologists began to find problems with the absolute application of homology, the basic principle upon which ancestral relationships were based.

Before the early 1880's, embryological morphology was dominated by the biogenetic law in its search for phyletic relations and a natural system of classification. The gastrula form was chosen as the starting point for the research, earlier segmental stages dismissed as having little importance for later investigations. Most studies included only a cursory description of "typical" cleavage patterns, delamination of cell layers, migration of pre-gastrula cells and invagination processes.[7] However, as more investigations were conducted on embryological events it became increasingly evident that the theorized homology of all germ layers and the uniformity of developmental phenomena was not wholly correct. Specifically, it was soon realized that embryologists needed to investigate the germinal layers of individual organisms without reference to the ancestral gastraea form. In addition, other observations indicated that there were valuable pro-morphological relationships to be studied in the segmenting ovum. In particular, it was determined that relations of symmetry existed between early cleavage stages and the adult body that gave significance to studies of early developmental stages. Both the problem with the germ theory and the new importance of segmental stages created a new interest among morphologists for studies of the pre-gastrula embryo.

> The relationship of the inner and outer layers in the various forms of gastrulas must be investigated not only by determining the relationship to the adult body, but also by tracing out cell-lineage, or cytology of the individual blastomeres from the beginning of development.[8]

By the late 1880's and early 1890's embryological morphology illustrated a marked attention to early development and a tendency not to refer to the ancestral gastraea form.

Problems with germ layer homology represented only one facet of the tendency to re-evaluate the ancestral aspect of morphology. The type of morphological speculation that was represented by Balfour and Gegenbaur and their reliance upon recapitulation, pushed embryological morphology beyond its legitimate limits.[9]

> In the mean time, we may as well admit that in the application of the embryological evidence to the broader problems of

> descent the recapitulation theory has encountered so many difficulties, undergone so many modifications and limitations, that investigators have in a measure wearied of their wanderings through the scholastic mazes of ancestral and secondary characters, of palingenesis and cenogenesis, of primary and adaptive forms and the like, and have sought for new interests and fresh notions of study. This is clearly apparent in the changed character of the more recent papers in embryology, which devote far less attention than those of ten or fifteen years ago to "genealogische Betrachtungen" that once formed their inevitable climax. The relative decline of interest in genealogical questions is partly due, I think, to a healthy reaction against the inflated speculation into which morphologists have too often allowed themselves to fall; but it is also in large measure a result of the growing feeling that the solution of the broader problems of genealogy still lies so far beyond our reach that we would better turn for a time to the study of questions that lie nearer at hand and are, to say the least, of equal interest and importance.[10]

The dissatisfaction among the morphologists working around 1890 concerning the search for an universal ancestral form and various problems with the supposed monophyletic descent of the Metazoa, caused a reaction against large-scale genealogical questions. Instead, the morphologist turned his attention to detailed developmental studies of a descriptive nature. Still, not all considerations of the historical record of species were abandoned. But these treatments of developmental studies were conducted in a much more restricted and controlled manner. In many cases, embryological work was accepted as valuable without the application to ancestry.

Accompanying the gradual refinement of morphology was the rise of experimental studies applied to embryological events. Prior to the 1880's, questions of embryology were typically framed in reference to the organism's evolutionary past. Since the prevailing doctrine was "ontogeny recapitulates phylogeny," most developmental phenomena were considered as resulting from the explanations drawn from the biogenetic law. With the decline of this emphasis in the 1880's, new questions were asked. These questions basically addressed the causes of the production of ontogenetic forms in terms of external and internal causative factors. That is, regulative factors of embryological events were the subject of the studies. Investigations of this nature began in Germany in the early 1880's. The original experiments primarily examined the role of external factors in regulating early cleavage.[11] The impressive aspect of this work was that the experimentalist could ask a direct question of the embryo, design an experiment to test the question and receive an answer to his query. The impact of experimentation was widespread.

> . . . and it is perhaps not too much to say that at the present day the questions raised by these experimental researches on cleavage stand foremost in the arena of biological discussions, and have for the time being thrown into the background many problems which were but yesterday generally regarded as the burning questions of the time.[12]

This application of experimentation to embryological studies was not completely a reaction against genealogical work or against the general program of morphology. Rather, it should also be considered as the logical expansion or refinement of embryological studies. Prior to the 1880's, morphology and physiology were considered to be distinct and completely separate disciplines. The work of morphology was conducted in an observational and descriptive fashion while physiology often involved the application of the experimental method. The subjects for study were also different. The morphologist was primarily concerned with descriptions of organic structure and form. Physiologists dealt with chemical and physical characteristics of body fluids and organic machinery, or questions of function. The interrelationships between these studies were few. A cogent example of this was the establishment of the Biology Department at Johns Hopkins. Brooks was hired to his position to balance the physiological biases of H. Newell Martin. In the early years there was very little interchange between the two programs since Martin dealt primarily with medical students and Brooks trained the naturalists. Even the advanced degrees awarded from the department were listed under distinct titles.[13]

This distinction between the application of morphology and physiology began to fade when both the morphologists and the physiologists began to venture into investigations of cellular activities. There was an increasing awareness that the events of the cell had both a morphological and physiological interpretation that was complementary. In terms of embryological research, this often involved the application of the methods of physiology that included experimentation, to the studies that had previously been considered strictly in descriptive terms.[14] It was this application that opened a whole new and fruitful field to scientific investigation.

> The accumulation of embryological facts and their application to problems of animal morphology from the days of von Baer to the period of Balfour's textbook of Comparative Embryology was carried on with ever increasing speed culminating in the present day when the revision of Balfour's work by Korschelt and Heider assumes such unexpected proportions. Though the advance of descriptive embryology has been so great, the physiological aspects of the subject have been but little cultivated, partly to be sure, from the necessary dependence of such work upon the anatomical facts that were not at first available. Now, however, when the normal development is known for all groups of animals and comparative embryology stands upon a firm basis, the application of physiological methods and the introduction of experimentation into a field promising much richer harvest than the study of adults can hope to yield, may be no longer delayed.[15]

Experimental methods, therefore, offered the possibility to direct embryological studies to additional areas of interest.

The most dramatic application of the physiological techniques or experimentation to morphology took place in the 1880's at the Stazione Zoologica di Napoli (the Naples Zoological Station). The station was established in 1872 by Anton Dohrn at the location that had been used by many European scientists to conduct marine studies. Dohrn was a former student and then colleague of Ernst Haeckel at the University of Jena. His original vision was to provide a location in which morphologists could work year-around in an institution dedicated to the great problems confronting biology. In the early years, the primary emphasis was to provide a description of the local marine forms. This effort resulted in numerous volumes of Fauna e Flora del Golfo di Napoli in which essentially all the representative groups of organisms found in the Naples region were described. These studies were augmented by more experimental work in the 1880's. Many of these subsequent studies were modeled after or received their initial impetus from Pflüger's gravitation work on cell cleavage. The investigators involved in this work, most of whom spent much of their time in residence at Naples, included August Rauber (1841-1917), Wilhelm Roux (1850-1924), Oskar Schultz (1859-1920), Richard Hertwig (1850-1937), Oskar Hertwig (1849-1924), L. Chabry (1855-1893), Theodor Boveri (1862-1915) and Hans Driesch (1867-1941).[16]

Perhaps the most influential early experimental work conducted at Naples was that done by Roux and Driesch. In a series of experiments begun in the early 1880's, Roux demonstrated by experimentally separating the blastomeres during early cleavage stages that differentiation in development was qualitative. In other words, specific embryonic cells received specific "germs" that indicated the eventual fate of that cell. Roux referred to this as the mosaic theory of development since the blastomeres were differentiated early in development. Studies investigating these embryonic stages by experimental procedures made up Roux's new field of *Entwicklungsmechanik*,[17] or developmental mechanics. Driesch attempted to duplicate the work of Roux. Applying the same *Entwicklungsmechanik* approach, he found that the early cleavage stages resulted in an equal distribution of cellular material. Differentiation took place following cell division through the interaction of the parts of the developing embryo.

> . . . the character of the individual cell is determined by its environment--i.e., by its relation to the whole of which it forms a part.[18]

Driesch referred to differentiation as a regulative process, since all the early blastomeres received the same material basis for development. His work was in direct dispute with Roux's claim to the mosaic nature of the segmenting ovum.[19]

The experimental program of developmental mechanics provided additional excitement to the descriptive studies at Naples. Many research programs followed the example of Roux and Driesch by investigating the early cleavage stages with experimental manipulations of the developing embryo. The experimental control of conditions that allowed the worker to provide answers to the question, "how does the organism do what it does?" certainly influenced many morphologists, particularly the younger ones, to look into such studies. It was into this environment that many of Brooks's students, including E. B. Wilson, Samuel F. Clarke, George Field (1863-1938), T. H. Morgan, H. Leslie Osborn (1857-1940), Ross G. Harrison and other important American biologists, were exposed by studying at Naples between 1881-1895.[20]

The influence of Naples was not solely restricted to the American investigators. Throughout the 1880's there was a drive mounted by the American biological community to establish a permanent seaside laboratory for the use of independent investigators and university research programs. The drive culminated in 1888 with the opening of the Marine Biological

Laboratory at Woods Hole.[21] With C. O. Whitman as the director (he had spent six months at Naples in 1881), the MBL was intended to adopt the most favorable aspects of other existing marine stations to fulfill best its task of producing more American investigators.

> The new lab at Woods Hole is nothing more, and, I trust, nothing less, than a first step towards the establishment of an ideal biological station, organized on a basis broad enough to represent all important features of the several types of laboratories hitherto known in Europe and America.[22]

Instruction was to be provided to students at the MBL, but the instruction was to be carried out by the investigators working at the station. Whitman was convinced, perhaps by his experiences at Naples and the Lake Laboratory of Milwaukee, that established investigators could provide the best instruction.

The initial work at the MBL did not indicate the immediate impact of Entwicklungsmechanik from Naples. Nevertheless, many of the major figures important in the development of the MBL recognized its debt to the model provided by Dohrn's laboratory. Most of the early work emphasized morphological studies of the flora and fauna characteristic of the Woods Hole area.[23] However, at the end of the nineteenth century, the application to morphology of the experimental method typical of physiology, came to characterize some of the research at Woods Hole. Undoubtedly the research techniques associated with Entwicklungsmechanik and the methods of physiologists who came to work at the MBL in the 1890's, most notably the cellular physiologist Jacques Loeb

(1859-1924), played an important role in demonstrating the effectiveness of experimentation. Again, however, it would be inaccurate to describe the growth of the experimental studies as an overt replacement of the descriptive work or as demonstrating a decline in studies of a more descriptive nature. Indeed, much of the experimental work was based upon the foundation of morphological research, an observation E. B. Wilson made.

> I do not belong to those who, impressed with the rich fruits and still greater promise of the experimental method, regard the past achievements of comparative morphology as labor lost, and look forward with indifference to its future. If its present methods are defective, they must be reformed; but the great body of facts it has accumulated, and will accumulate hereafter, will always form the very framework of biological science.[24]

Furthermore, Wilson recognized the intimate relationship between embryological morphology and experimental physiology. For example, the controversy surrounding the Roux-Driesch experiments on cell differentiation could only be attacked by the new methods of experimental investigation in embryology.[25] This same viewpoint was shared by C. O. Whitman.

> Experimental biology represents not only an extension of physiological inquiry into all provinces of life, but also the application of its methods to morphological problems; in short, it covers the whole field in which physiology and morphology can work best hand in hand.[26]

By the early and mid-1890's, the impact of the problems with the germ layer, the rise of experimentalism in biology, the influence of the program of Entwicklungsmechanik and the establishment of the MBL as a research facility, all served to affect markedly American biological investigations. While in a sense the

1880's were dominated by morphological questions that were best illustrated by the work of Brooks and his students, in the 1890's the situation became incredibly more complex. These end-of-the-century studies represented such a proliferation in the questions and methods that any characterization of the work in a general sense is impossible.

Unfortunately, it is difficult to appraise Brooks's exact position during this change because of several factors concerning his personal life. Due to his own ill health and the declining health of his wife, Brooks was able to direct only the summer sessions of the CZL in 1891 and 1894. It was during these summer sessions that Brooks conducted his major scientific work. Therefore, it is not surprising that his research productivity, as evidenced by publications in scientific journals, essentially ceased in the mid-1890's. These same health restrictions also limited Brooks's work in Baltimore. His marine work received an additional set back in 1897 when yellow fever killed two members of the CZL working in the Bahamas. As a result, the trustees of the University refused to provide additional funding for the laboratory. The needs of the students were met by obtaining a subscription to work at Woods Hole, the Fish Commission Laboratory at Woods Hole or the Commission's new laboratory at Beaufort. Brooks was, however, unable to accompany his students to most of these sessions. His seaside work effectively ceased until he took two trips to study tunicates in the Dry Tortugas in 1905 and 1906.

Nevertheless, Brooks's role as America's premier morphologist was important for developments in American biology not only prior to the 1890's but well into the twentieth century. Although we have previously discussed Brooks's influence as a teacher upon many of America's foremost biologists in Chapter Two, his importance in this area must be stressed.[27] Admittedly, one cannot observe a close connection between the research of Brooks in pure morphology in the 1880's and the experimental researches of some of his most prominent students in the 1890's and the early 1900's.[28] However, many of the descriptive studies of Wilson, Andrews and Conklin tracing cell-lineage in development and constructing cell maps, can be pictured accurately as the logical extension of the earlier descriptive morphology work in development. Furthermore, the fact that Brooks emphasized investigations of the developmental stages of marine organisms was also important in influencing the nature of much of his students' later research. Wilson, Andrews, Conklin, Harrison, Morgan, Bateson and others conducted much of their experimental and descriptive work on marine forms. In addition, many of the students, undoubtedly through their summer experiences at the CZL, recognized the value of marine stations in which this type of research could be conducted. Naples and the MBL became the frequent centers for work by Johns Hopkins graduates. In fact, eleven of Brooks's students became actively involved in the affairs of the MBL by serving on the Board of Trustees.[28]

Brooks, himself, had been a trustee from 1893-1908. Brooks also stressed a thorough acquaintance by his graduate students with the current literature and important biological classics. The reading of these works and discussions of various topics at the Morphological Seminary was important in providing Brooks's students with the awareness of the major biological issues, a characteristic for which they became noted.

It should be stressed that many of the problems confronting morphology in the 1880's were problems that Brooks recognized and addressed in his research. Therefore, it is not surprising that Brooks's students also considered these problems. For example, Brooks's skepticism concerning the search by morphologists for a hypothetical ancestor for all the Metazoa or for the monophyletic descent of vertebrates from an invertebrate stock was shared by his students.

> Almost every group of invertebrates that was intensively studied by any zoologist was found by him to have certain features that suggested relationship to the vertebrates. Thus Adam Sedgwick argued for a coelenterate ancestor, Hubrecht for nemertean, Dohrn for an annelidan, Gaskell for a crustacean and Patten for an arachnidean origin. All graduate students at Johns Hopkins were expected to read these classics on the ancestry of the vertebrates. I felt that the mollusks had been neglected in these speculations and once jocosely suggested relationships to chordates, and [that] the larvae of the chordate, Balanoglossus, resemble larvae of the echinoderms. Thus almost every phylum showed certain resemblances to vertebrates, and personal predelictions decided which branch of your family tree you chose to emphasize. Reflecting on this chaos of speculation Watase (another of Brooks's students) once said to me, "I am done with this whole phylogeny business."[29]

Likewise, Brooks's requirement that homologies have a more exact basis than solely in reference to the community of descent from an ancestral gastraea was adopted by his students. Brooks's treatment of this problem was to trace the homology back to its common origin in a shared ancestral form of the group under investigation. E. B. Wilson and E. G. Conklin attempted to refine this method by studies of cell lineage. Blastomeres of the early cleavage stages were numbered and carefully observed throughout embryonic development. This technique enabled these workers to show the exact cell origin of cell layers and organs in a manner that the theory of germ layers was unable to do.[30]

> The subject of germ layers is no longer so important as it was once considered; in fact, the theory of the homology of the germinal layers has met with so many difficulties of late that it is now generally maintained only in a greatly modified form. However, the fundamental idea which was prominent in germ-layer discussions is of vital interest today. In the whole history of the germ-layer theories I see an attempt to trace homologies back to their earlier beginnings. This problem is as important to-day as it ever was, and whether one find these earliest homologies in layers or regions or blastomeres or the unsegmented ovum itself, the quest is essentially the same.[31]

In other words, work on cell lineage provided the morphologist with a more exact method of determining homologies. Consequently, Conklin's and Wilson's work was an extension of the homological work of Brooks.

Brooks, however, did not immediately recognize the value of cell lineage. He made the following remark to Conklin when he was presented with the cell lineage proposal for a thesis topic.

> 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 there is any morphological significance in it.[32]

Brooks still allowed Conklin to complete the project and then explained his rationale to his student.

> Well, Conklin, this University has sometimes given the doctor's degree for counting words [a humorous remark directed at Professor Gildersleeve, Brooks's longtime friend at JHU and a professor of philology]; I think maybe it might give one degree for counting cells.[33]

This remark was probably made more in humor than in seriousness for Brooks came to recognize the cell lineage work as a valuable tool in morphological study. Wilson demonstrated the application of such work to the type of research program that was typical of Brooks.

> A large part of the work in cell-lineage during the past ten years has been devoted to a comparison of the morphological value of these quartets of cells in the annelids, mollusks, and platodes [Platyhelminthes]; and the remarkable and interesting fact is now becoming apparent that while they do not have exactly the same value in all the forms, they nevertheless show so close a correspondence both in origin and in fate that it seems impossible to explain the likeness save as a result of community of descent.[34]

Certainly Wilson's remarks concerning the correspondence of the cell quartets between different animal groups, coming at the end of the 1890's, do not differ significantly from Brooks's comments concerning ancestry in the 1880's.

Perhaps one of the most striking influences Brooks apparently had upon his students was the need to study organisms in relation to their environment. He constantly referred to the reciprocal interaction between the organism and its surrounding.

It was only in reference to this relationship that the morphologist could understand the natural phenomena. Thus, Brooks emphasized an organismic approach to biological investigation. Studies that examined living organisms only in the laboratory or studies that investigated cellular activities apart from their role in organic structures, were incomplete.

This same approach characterized the work of all of Brooks's graduate students, both while they were in residence at Johns Hopkins and after they left the University. Ross G. Harrison stated that in conducting research the experimenter could not understand the parts of an organism without looking at the whole organism, the effects of the parts on each other, and the effects of the parts on the whole.[35] In E. G. Conklin's description of the role of protoplasm in problems of cellular differentiation, he maintained there was no evidence that supported the claim for a simple physical or physiological explanation. Instead, the cell acted as a whole and the interaction of all its parts were essential for the "causes of all vital phenomena."[36] E. B. Wilson provided a similar viewpoint.

> Every living being, at every period of its existence, presents us with a double problem. First, it is a complicated piece of mechanism which so operates as to maintain, actively or passively, a moving equilibrium between its own parts and with its environment. It thus exhibits an adaptation of means to ends, to determine the nature of which, as it now exists, is the first task of the biologist.[37]

The second problem Wilson referred to represented another shared interest of Brooks and his students. A primary concern of

Brooks was that the biologist consider the events of ontogeny and phylogeny to be related; that is, phylogeny was a "series of ontogenies."[38] Ontogenetic development contained remnants of the ancestral history of the organism. Despite the claim that biological investigators were turning from questions of ancestry, there was ample evidence from several sources that these considerations still occupied the work of several of America's leading biologists. E. B. Wilson provided evidence that the historical record of the species was still important.

> But, in the second place, the particular character of this adaptation cannot be explained by reference to existing conditions alone, since the organism is a product of the past as well as of the present and its existing characteristics give in some manner a record of its past history. Our second task in the investigation of any problem of morphology or physiology must accordingly be to look into the historical background of the phenomena; and in the course of this inquiry we must make the attempt, by means of comparisons with related phenomena, to shift out adaptations to existing conditions from those which can only be comprehended by reference to former conditions. Phenomena of the latter class may, for the sake of brevity, conveniently be termed "ancestral reminiscences,"--though it may not be superfluous to remark that every characteristic of an organism is in a broad sense reminiscent of the past.[39]

Evidently Wilson did not consider morphology, physiology or questions of phylogeny to be inconsistent with each other.

Brooks's students also carried with them a deep appreciation for morphological or observational work. This characteristic was evident even among those students whose work became predominately experimental in nature. While this connection between Brooks and his students may be partially explained by their shared experiences at Johns Hopkins and the CZL, another factor was the recognition of the value that descriptive studies had upon biological questions. In Conklin's Crepidula work, he noted the value embryological morphology had upon experimental embryology.

> And yet, while fully recognizing the value of experimental embryology, we ought not to forget that "Nature is continually performing some very remarkable experiments in her own way," and I believe we need to know more about these normal processes before we can properly understand abnormal ones. . . . In any case the phenomena of normal development are the ones to be explained, whatever method may be used; and before any explanation can be given it is necessary to know the usual development as thoroughly as possible.[40]

In other words, to obtain any significant results from experimental manipulations of development, the investigator had to have an appreciation for normal development. Conklin stressed that because of the interrelationship between observation and experimentation, one could not draw a deep distinction between the two. Certainly neither method of investigation alone could make a sole claim of certitude regarding facts or causes.[41]

E. B. Wilson expressed similar views in reference to investigations concerning the role of specialized protoplasmic structures in determining the cell's physiological activity. Noting that the research continually pressed for the discovery of smaller units of organization to explain the various phenomena, Wilson retained a conviction for the value of morphological work on the cellular level.

> I would like, at the outset, to express the opinion that, if we except certain highly specialized structures, the hope of finding in visible protoplasmic structure any approach to an understanding of its physiological activity is growing more, instead of less, remote, and is giving way to a conviction that the way of progress lies rather in an appeal to the ultra-microscopical protoplasmic organization and to the chemical processes through which this is expressed. Nevertheless, it is of very great importance to arrive at definite conclusions regarding the visible morphology of protoplasm, not only because of its intimate connection with all the problems of cell-morphology, but also in order to find the right framework, as it were, for our physiological conceptions, and thus to gain suggestions for further physiological and chemical inquiry.[42]

Despite the apparent reduction of protoplasmic physiology to chemical activity, investigators like Wilson maintained that morphological studies of the ultra-structure were important. In fact, these studies had application to the physiological work.

At the same time that Brooks's students retained an interest in and for descriptive work, Brooks did not appear to be averse to the application of experimentation to morphological questions or to the rise of more experimental research. In the summer of 1881, Henry Sewall (1855-1936), who had received his doctorate in physiology from Johns Hopkins, attended the CZL at Beaufort to conduct physiological work. Brooks wrote to President Gilman expressing his enthusiasm for this type of investigation.

> I am very glad to have some one engaged in physiological research here, as almost nothing of the kind has ever been done with marine animals, although they present exceptional advantages for such work.[43]

Sewall was not the only physiology student to attend the CZL. Among the others were William T. Sedgwick, Christian Sihler (n.D.), W. H. Howell (1860-1945), H. H. Donaldson (1857-1938), Theodore

Hough (1865-1924), T. E. Shields (1862-1921) and Reid Hunt (1870- ?).

The many experimental studies conducted in Naples and the gradual application of these same techniques to embryonic studies, especially at the MBL in the later 1890's, were accepted by Brooks. In Foundations of Zoology Brooks referred to the experimental methods of Roux and Driesch and the value of these methods for embryological research.

> Embryonic development is so delicate and so complicated that we cannot hope to trace, far less to imitate, the action of these stimuli in anything like their natural perfection; yet we can, now and then, rudely imitate some of them, while, in other cases, we can demonstrate their presence and influence indirectly by preventing them from acting. Some eggs which have begun their development by division into two, four, or eight cells, may be shaken apart without destroying their vitality, and when thus separated, a cell which would normally have given rise to half or quarter the natural size. Embryologists are rapidly adding, by experimental methods, to our knowledge of the mechanics of development, and it has been known, since the day of Aristotle, that some of the latest stages in the development of the higher animals and of man do not take place in the absence of certain normal physiological stimuli.[44]

Brooks did not apply these techniques to his own research, primarily due to the paucity of his research following the mid-1890's when the new methods were widely employed. However, Samuel Rittenhouse (1873- ?), a student of Brooks, included in his research on the embryology of *Turritopsis nutricula* the blastomere separation experiments of Boveri, the Hertwigs, Roux, Driesch, Wilson, Morgan and Loeb.[45] The experiments were designed to determine the effect of separating the egg at the early stages of cleavage since *T. nutricula* was characterized by irregular segmentation, loose blastomere connection and a tendency to separate into definite lobes at the early cleavage state.[46] Since Brooks was a co-author and the research director of the project, it is not unreasonable to assume that he approved of the experimental methods. In fact, Brooks noted in 1907 that the trend toward providing an experimental base for developmental studies was an advance over the previous work.

> The gradual disappearance of attempts to invent evolutionary hypotheses to account for individual development, or ontogeny, and the return to a more epigenetic standpoint, based on experimental evidence that the ontogenetic development of eggs can be understood only through their reciprocal interactions with their internal and external environment, seem to me to be a notable reformation.[47]

Therefore, it must be maintained that while Brooks restricted his own work to the methods of descriptive methodology, he was not opposed to the innovative methods of experimental biology that characterized some of the embryological work at the very end of the nineteenth century.

Brooks's strong philosophical bias and interest in considering problems in a larger framework was undoubtedly of some influence on his students. During the summer sessions of the CZL and through the discussions both at Johns Hopkins and sessions of the Morphological Seminary held at "Brightside" these questions were posed. Often the works of Darwin, Wallace, Weismann, Haeckel, Lankester, Balfour and others that were included on the graduate reading list were discussed. At other times, general topics such as evolution, variation, heredity, etc., were the topics of conversation.

> 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. . . . 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.[48]

Brooks used the same opportunities to discuss his own work with his students.

> As I recall his reading to me of the then unfinished manuscript of his book on Heredity in my room on Centre street in 1876, of the many long talks on biological subjects, in either his room or mine at the University, at Brightside, or at Crisfield, Fort Wool or Beaufort, I became aware again of the constant seriousness, and power of his thought, which awoke and continually increased an admiration for his intellectual ability.[49]

Many of the subjects Brooks discussed with his students became primary interests of the students. For example, William Bateson, who spent the summers of 1883 and 1884 with the CZL at the urging of Adam Sedgwick to study Balanoglossus, maintained that his exposure to Brooks influenced him as nothing in his educational experience had before.

> Many of Brooks' pupils must look back on similar pleasant hours of intimate, informal summer laboratory life as critical moments in their development. For myself I know that it was through Brooks that I first came to realize the problem which for years has been my chief interest and concern. . . . To me the whole province [heredity] was new. Variation and heredity with us had stood as axioms. For Brooks they were problems. As he talked of them the insistence of these problems became imminent and oppressive. It all sounded rather inchoate and vaporous at first, intangible as compared with the facts of development which we knew well how to pursue, but with the lapse of time the impression became strong that Brooks was on the right line.

> That autumn I went home feeling that though in technique we were a long way ahead of Johns Hopkins . . . yet somehow Brooks had access to novelties of a more serious description.[50]

Like Bateson, Brooks influenced Conklin's interest in evolution. This was not through the mere required reading of the Origin of Species, but through the long discussions concerning the many intricacies of Darwin's theory. This topic became one of Conklin's prime areas of biological concern. Conklin's own treatment of evolution theory illustrated his debt to Brooks.

> But the theory of evolution includes much more than the doctrine of descent; it is an attempt to explain by natural causes the wonderful adaptations of organisms to their conditions of life. The greatest problems of Biology do not center in the structure of organisms, nor in their functions, nor even in their origin, but in their fitness. Life is, as Professor Brooks insists, "response to the order on nature," and it is this element of useful, purposive response which more than anything else distinguishes the living from the lifeless and separates the methods of Biology from those of Chemistry and Physics.[51]

The summer sessions of the CZL provided many Johns Hopkins students with the opportunity to study marine organisms in detail and to become well-acquainted with Brooks. While attendance at the sessions was mandatory for the graduate students in zoology, the evidence suggests that most of them thoroughly enjoyed the experience. Again, in addition to the field work and laboratory discussions, topics of biology were widely discussed and more intensive reading bearing on research problems was encouraged. All the work was expedited by a sense of comaraderie, facilitated by the fact that all the students and Brooks lived in a communal arrangement. These accommodations were accepted with enthusiasm by the students but often proved to be a source of irritation for Brooks.

> . . . and finally I am running the mess and have thirteen hungry men to feed every day in a place where there are no markets, and I can never tell until the tide turns whether there is to be any thing for dinner. Keeping a boarding house from love of science is as thankless a job as doing the same thing for profit, and I have to submit to as much criticism as if I were making my fortune. I never had as many good workers here before, but I never had as much fault found with the mess; and although I try to pay no attention to it, I do find it very troublesome.[52]

Brooks's primary influence at the CZL was outside of the kitchen. Although his approach at the summer session was to allow the student to pursue his own investigations, Brooks's personal research activities served as an example for the younger workers. In the summer of 1884 Brooks was unable to attend the early part of the CZL because of an illness. In his place, H. W. Conn served as "assistant in charge" and related his feelings concerning Brooks's absence.

> We miss Dr. Brooks very much. The laboratory hardly seems complete without him. His valuable advice, his fertile suggestions, and above all his example as an investigator cannot be supplied by anyone here this summer. It is rather unfortunate also that there is no one here to engage in work of economic nature [oyster work]. We are all of us young, and as yet students who must learn the rudiments of science and scientific work. . . . I think therefore that we have opened the Summer under favorable auspices, and although we can hardly expect the same amount of work done as is usual, owing to the absence of Dr. Brooks. . . .[53]

Conn mentioned in a later letter of the same summer that the work of the CZL was "handicapped by the absence of Dr. Brooks."[54] In the preceding summer, E. B. Wilson made the following comment concerning the reaction of several investigators from Harvard who were working at the CZL.

> The Cambridge men seem to be agreed that nothing had done more for them in biology--at least so far as Morphology is concerned--than their connection with this laboratory.[55]

The character of the CZL was largely the product of Brooks's research interests. The various research projects that were undertaken were often suggested by Brooks. Many of these suggestions represented studies that Brooks had initiated but had allowed graduate students to complete. Osborn's studies on prosobranchiate gills, Herrick's work on the development of Alpheus, Bigelow's research on Cassiopea, Lefevre's investigations of budding in Peropora, Rice's observations on Amphioxus and Rittenhouse's work on Turritopsis were all projects that Brooks allowed his students to assume. William Bateson expressed his appreciation for this unselfish character.

> With a magnanimity, that on looking back I realize was superb, Professor W. K. Brooks had given me permission to investigate it [Balanoglossus], thereby handing over to a young stranger one of the prizes which in this age of more highly developed patriotism, most teachers would keep for themselves and their own students.[56]

It was not only Brooks's students who realized the influence he had over the nature of the activities of the CZL. He was recognized in the American biological community as one of the leaders in marine research. Joseph LeConte (1823-1901), the professor of geology and natural history at the University of California in Berkeley, wrote with eagerness to Brooks concerning a possible trip by Brooks to California. LeConte identified Brooks as

> . . . some one who can tell us and show us what modern Biology is, and also stir up the Regents on the subject of a Marine Station.[57]

Brooks was also the early choice of the trustees of the Marine Biological Laboratory for the position of director.[58] However, for reasons that have not been uncovered, Brooks turned the position down, a decision the trustees "all regretted."[59]

While all of the foregoing remarks have been intended to provide an indication of Brooks's importance in the development of American biology through the many students he influenced, it must be admitted that many of the examples have yielded only circumstantial or tenuous evidence to support the claim. Nevertheless, it was not a mere accident or historical coincidence that such eminent biologists as E. A. Andrews, E. G. Conklin, Thomas H. Morgan, E. B. Wilson, Ross G. Harrison, William Bateson and D. H. Tennent were drawn to study with Brooks and became products of the instruction available at the Biological Laboratory of Johns Hopkins. Regardless of the precise nature of the influence, the fact that these men shared common interests in embryological studies, they worked extensively with marine organisms, they all adopted an organismic orientation in their investigations, they valued morphological work in its descriptive bearing upon experimental studies and they had life-long interests in the more philosophical nature of biology, can be attributed to their common educational experience. Certainly many of these men attributed such an influence to their mentor. At a memorial dinner on December 31, 1908, shortly after Brooks's death, many of Brooks's former students and colleagues penned the following comments on their relationship to Brooks.

> He lived the simple life of the true naturalist; thus leading us by example and by vividly picturing, through a wonderful gift, the truths of Biology and the charm of this study. Henry McE. Knower (1868-1939)

> His influence upon my thinking has increased with my growth in experience. D. H. Tennent

> William Keith Brooks was my greatest teacher in my student days (1893-97) and equally so when in later years my turn came to train others. Duncan S. Johnson (1867-1937)

> In grateful recognition of my obligations to a stimulating teacher, a calm and broad-minded investigator, and a loving friend. E. G. Conklin

> With memories of many happy & fruitful days, & with grateful acknowledgement of what I owe to a wise and rare teacher. E. B. Wilson

> Dr. Brooks was, I think an inspiring and successful teacher because he lived in intimate and personal relationship with his students, who remember him not only as a philosopher but also as a friend. T. H. Morgan

> I am glad to add a word of tribute to the memory of my friend--the wisest and most profound of American zoologists--"a Sage in Science" as I had once occasion to call him--and withal one of the most helpful of teachers and most sincere of friends: in the thirty five years of our acquaintance from Penikese in 1873 to Baltimore in 1908. David Starr Jordan

> To W. K. Brooks, who in the laboratory and in his hospitable home set to grateful pupils an example of philosophical thought based on patient research. Robert Payne Bigelow

> In memory of William Keith Brooks, the prince of American zoologists--an apostle of progress, truth and right; yet a man among men. Samuel Rittenhouse

> My gratitude to Professor W. K. Brooks for his profound and clear thinking, for his sincere and skillful guidance in the study of nature, and for his friendship. H. V. Wilson

> Lastingly indebted to Professor Brooks not only for guidance as a student but for inspiration from his discriminating judgement and his rare, whole-souled devotion to his chosen work. Maynard M. Metcalf (1868-1940)

> I am keenly conscious of the fact that Professor Brooks, far more than anyone else, set for me by his example the ideals which I have attempted to follow in scientific work. George Lefevre[60]

The above remarks made by many of Brooks's most well-known students provides corroborative evidence to support the claim of Brooks's influence upon his students. Certainly it is clear from these statements that many of these men felt that Brooks had an impact upon their scientific lives.

To denigrate Brooks's position in the development of American biology by stressing the fact that his most important students worked in areas outside of descriptive biology[61] and to minimize the importance of morphological studies on the growth of experimental biology,[62] creates an inaccurate portrayal of events at the end of the nineteenth century. It leads to the impression that in the 1890's American biologists turned away from descriptive studies in morphology and chose instead to work upon completely new and different experimental questions. An examination of American biology at the end of the century indicates this inaccuracy.

As has been pointed out earlier in the study, the major thrust of morphological work was in embryology. Prior to the 1880's, investigations were dominated by phylogenetic considerations from embryological evidence. The descriptive studies traced development back to the gastrula type and then examined the various embryonic stages for evidence of homology. Severe problems with these ancestral concerns forced the morphologists to refine their techniques and practices. The results of the refinement was the emergence of the cell lineage studies that investigated the intricacies of cleavage and early germ layer formation.[63] This new method of investigation allowed the morphologist to overcome the problem of describing homologies from the common descent from primary germ layers. Investigators instead looked at the pre-gastrula stages of development to determine the exact origin of cells, tissues and organs from the segmenting ovum or blastomeres.

The cell lineage work, pioneered primarily by E. B. Wilson, E. G. Conklin and C. O. Whitman, served to refine embryological morphology to a level of sophistication that a distinct discipline of embryology could be identified. Conklin observed:

> Now that we know the exact cell origin of these layers and organs, it will never again be possible in describing the development of these animals to refer the origin of certain organs to "germ layers" merely, nor to refer the origin of these layers to certain general regions of the embryo. The importance of this line of work, not only in the study of the groups named, but also to the science of embryology as a whole, is fully recognized both in this country and abroad. . . .[64]

Still, these studies of cell lineage were, like early morphological descriptions of development, completely descriptive. In this regard, these embryological studies represented a continuity from the earlier work. Additionally, not only did these studies have their origin in morphology, but the same methods continued to be applied to embryological work well into the twentieth century. An examination of issues of the Journal of Morphology provides testimony to the pervasiveness of this work.[65]

The cell lineage work was impressive. Homology problems within distinct taxonomic groups were eliminated by the success of referring embryonic structures to the primitive blastomeres. Furthermore, this method illustrated the reasons for the inadequacy of the germ layer hypothesis. At the stage of germ layer formation, differentiation had already been so well established that the layers represented distinct embryological regions. Only by referring to the initial stages of embryonic development could the embryologist observe distinct morphological units (blastomeres) that would exhibit uniform and reliable homologies. The thrust at the MBL was, as a result, toward encouraging studies of development that looked at the maturation stages of sperm and egg, the fertilization events and early cleavage formation. With cleavage, the embryologist could distinguish and define the early blastomeres, trace the fates of the blastomeres and their succeeding derivative cells, and develop embryonic "mappings" for the cell and tissue origin.

Because of the method of cell lineage studies, the nature of these investigations was decidedly descriptive. In application, however, these studies were important not only for their significance to descriptive embryology, but also in the experimental work. Neohide Yatsu (1877- ?) expressed the dual concern of these studies in his work on the embryology of *Cerebratulus laeteus*.

> Five year [ago] Professor Wilson suggested to me to make a careful study of maturation, fertilization and early cleavage stages of the egg of Cerebratulus laeteus, partly in order to clear up some disputed cytological problems and partly to give a morphological basis for my work on experimental cytology and embryology.[66]

Several other investigators also referred to the application of these studies and also noted the encouragement for more of such work from investigators like Wilson and Whitman. Howard E. Enders (1877-1958) noted the "interest and friendly counsel" he obtained from Brooks on his work concerning the development of Chaetopterus variopedatus.[67]

Yet, even with the refinements that took place in descriptive embryology, many of these studies contained remnants of the aspirations of the morphological program. Several embryologists, particularly those who had been variously associated with Brooks, still referred to the phylogenetic significance of homologies based upon the new cell lineage work. E. G. Conklin noted that the studies he conducted and similar studies undertaken by E. B. Wilson and Frank R. Lillie (1870-1947) revealed a fundamental similarity in the developmental history of individual blastomeres. This suggested to Conklin that the resulting resemblances of the species was due to resemblances of protoplasmic structure within the blastomeres. In wording that illustrated Conklin's debt to Brooks's school of morphology, he expressed the implications of these resemblances.

> If such resemblances between blastomeres are homologies, what follows? (1) Cleavage has a certain phylogenetic significance, and, although possibly more liable to

> modifications than larval or adult stages and hence, less trustworthy as a test of homology and of genetic relationship, it may in certain cases at least preserve ancestral conditions even after they have disappeared in end stages (annelids and mollusks). Incidentally, the homologies of cleavage added to those embryonic and larval structures indicated the close relationship of annelids and mollusks, whereas the entire embryological history only serves to widen the gap between the cephalopods and other mollusks.
>
> (2) The early cleavages are morphologically more important than later ones. This follows from the notion of determinate cleavage, some of the earlier blastomeres being destined to form entire regions or organs of the animal, but principally from the fact that the earlier cleavages are more constant than the later ones.[68]

In 1886, investigators of cell lineage were still including considerations of phylogeny, or at least, phylogenetic implications of the ontogenetic work.

E. B. Wilson echoed Conklin's attitude toward cell lineage work. Wilson stated that the studies of annelid and mollusk cell lineage revealed a common method of mesoblast formation. He continued on to suggest that the similarities were so marked that they indicated the shared origin of the two groups. The evidence came from the fact that in the formation of the blastomeres, both the annelids and mollusks exhibited the disappearance of entoblasts by forming a purely mesoblastic fourth quartet.

> Second, the phenomena we have considered seem to leave no escape from the acceptance of ancestral reminiscence in cleavage, with all that that implies.[69]

Again, Wilson illustrated the connection between ontogenetic studies and implications of phylogeny. For him, the principle significance of cell lineage work was the determination of the common origin and fate of cells.[70]

In an article written in Science in 1905, Conklin continued to include questions of phylogeny in studies of ontogenetic development. He noted the specific nature of eggs from different phyla, but suggested the possibility of a relatedness between these types.

> . . . in particular the localizations in the eggs of ctenophores, nemerteans, echinoderms, annelids, mollusks and ascidians are thoroughly characteristic of each phylum, and except in the case of the annelids and mollusks there are few similarities between these types. Nevertheless, it is possible that certain of these types may have been derived from others; in fact, such transformations might be accomplished far more easily in the egg than in the adult.[71]

However, Conklin and the other investigators at this time did not leap to the wholesale speculations that were characteristic of some of the earlier studies. Much like his mentor at Johns Hopkins, Conklin was very skeptical about the value of such theories. But, also like Brooks, Conklin believed that the evidence of embryology provided a basis for the assumption that at some stage in evolution relationships between taxonomic groups did exist.

> Despite the evident and almost insuperable difficulties involved, certain zoologists have not hesitated to indicate how the adult form of one phylum might have been derived from the mature form of another; thus we have the coelenterate, the nemertean, the echinoderm, the annelid and the arthropod hypotheses as to the origin of the vertebrates, and in each of these cases by stupendous transformations, degenerations and new formations of the adult form of the invertebrate in question the vertebrate is supposed to have sprung into existence fully formed and panoplied, like Minerva from the brain of Jove. In all these speculations fancy occupies so prominent a place and facts are so scarce that it is no wonder that the whole "phylogeny business" has come into disrepute. Nevertheless, the evolution idea compels us to assume that there are relations more or less remote between all phyla and that

> some must have come from others by natural processes. Without attempting to defend any of the hypotheses mentioned it may be here pointed out that relatively slight modifications in germinal organization would convert one type into another.[72]

From this selection it is evident that as late as 1905 investigators who were working at the forefront of biological research still maintained an interest in questions of ancestry. This was especially marked among the embryologists who received their early training from Brooks.

While cell lineage studies became a major interest at the end of the nineteenth century, several American biologists also became interested in experimental studies of development. As was pointed out earlier, this new direction was primarily influenced by Entwicklungsmechanik, associated with Roux and Driesch at Naples, and by the application of methods from physiology to embryological studies. In the United States, the new movement was popularized by T. H. Morgan. In an article written in 1898, Morgan cited the initiation of this new field of study "in the last few years."[73] Entwicklungsmechanik was the study of the causal morphology of the organism or the investigation of the changes through which the embryo passes as a result of a series of causes. The causes of the changes were the subjects of the new area of research.[74]

Morgan did not view the new field of study as replacing descriptive studies of embryology. In fact, it was this same work that provided the groundwork for developmental mechanics.

> We see the egg segment and then form a blastula, gastrula and larva. Descriptive embryology gives a series of pictures of these different stages. The more complete the series the fuller will be our knowledge.[75]

Entwicklungsmechanik represented the application of experimentation to the descriptive studies. Referring to the experiments of Pflüger and Roux, Morgan demonstrated how experimental researches could ask questions descriptive studies could not entertain. Consequently, he believed the application of the methods of physiology to embryology served to form a new approach to the study of embryology, experimental embryology.

American biology in the 1890's was becoming much more sophisticated with the application of new methods of biological research. In terms of experimentation, the new methods continually reinforced the relatedness of different approaches.[76] The real change in American biology that became evident from 1880-1900 was not, therefore, the abandonment of the morphological program and the universal acceptance of experimentalism in biology. Instead, this period was characterized by the application of experimental methods, through the already established field of physiology, to morphology. E. B. Wilson noted this change.

> For my part, I am wholly ready to admit that the introduction of experimental methods into morphology is the most momentous step in biological method that has been taken since the introduction of such methods into physiology by Harvey and Haller.[77]

He was quick to point out, however, that the change did not abrogate the role of descriptive biology.

> Observation and experiment give us our materials, but it is the comparison and correlation of those materials that first build them into the fabric of science.[78]

Wilson held to the common thesis of American biologists that the scientist must draw upon both the results of morphology (or descriptive embryology) and experimentation (or experimental biology).

The impact of experimentation on biology should not be minimized in stressing the value of the descriptive work. Indeed, it was the application of the program of the physiologists that proved to be so influential that the work in pure morphology was often not as well publicized.[79] At the same time, one cannot obtain a reliable impression of the biological work in the 1890's by referring to the apparent distinction between physiology and morphology or experimentalist and naturalist. Instead, this period must be looked upon as a time in which distinct sub-disciplines were developing in biology.

Prior to the 1890's, American biology could be accurately described as being characterized by the study of morphology. It was in terms of morphology, in fact, that essentially all biological investigation was described, with the exception of the medically-oriented physiology. This changed dramatically in the 1890's as the result of problems with the foundations of morphology and the success of experimental studies. The cell lineage work that characterized the research at Woods Hole led to the formation of descriptive embryology or developmental biology. Wilson, Conklin, Whitman and others were instrumental in making embryology a distinct sub-discipline of biology. Another branch of investigation was physiological morphology. Under this program, work was done in regeneration studies, grafting of animal parts and studies of stimulus response. The most important workers in this field were F. R. Lillie, H. S. Jennings (1868-1947) and T. H. Morgan. Experimental embryology could also be distinguished as a unique sub-discipline. The work, stimulated by Entwicklungsmechanik and Jacques Loeb's studies on parthenogenetic development in sea urchins, was carried out at the MBL by E. B. Wilson, Nettie M. Stevens (1861-1912), D. H. Tennent, George Lefevre and Morgan. To these three well-defined areas of research must be added cytology, morphology and physiology. Cytology was not as well defined, but by virtue of E. B. Wilson's book, The Cell in Development and Inheritance, problems of a cytological nature were framed and directions for research were pointed out. There was a substantial amount of work done at the turn-of-the-century concerning the function of cell ultra-structure. Morphology, as has been illustrated, was still very much in evidence. Physiology also retained a prominent position as a distinct area of biological work.

The emergence of several new areas of work resulted in a more complicated picture of American biology. Each area had its own problems, methods and goals that made it a distinct enterprise. In addition, since many of the topics of research were novel, there was much excitement surrounding them. Certainly the late 1890's and early 1900's at the MBL reflected this exuberance. Studies on parthenogenesis, regeneration, stimulus response and embryo manipulation captured the investigators attention. Still, morphological work continued to provide the "very framework" upon which these other studies were based. Descriptive studies of development, utilizing cell lineage techniques served to direct much of the embryological work, both descriptive and experimental.

The continuation of embryological morphology or descriptive biology was evident in the publications from the end of the nineteenth century. Of course, the Journal of Morphology continued to print articles that were of a definite morphological nature. However, the journal also published several articles that can be recognized as cytological, as well as one on experimental work in early cell cleavage by Jacques Loeb (1892). The Proceedings of the Boston Society of Natural History underwent a gradual change from evolutionary natural history articles prior to the 1890's to articles that emphasized the developmental history of organisms. Although the journal retained a natural history focus, examinations of volumes after 1895 revealed the inclusion of many papers on embryological morphology. E. B. Wilson published his article on questions of the mechanism of inheritance, "Karyokinesis and the fertilization of the ovum" in 1895. The American Naturalist was also primarily concerned with natural history and evolution prior to 1890. In 1885, the journal began to include a section in "General notes" on embryology as distinct from zoology and physiology. Both zoology and embryology were descriptive, while the physiological articles were functional. Following 1885, the journal began to carry more articles that reflected the leading research in American embryology. In 1890, E. A. Andrews, who served on the editorial board, included descriptive reports of many of the more important descriptive and experimental research activities that were being undertaken in America and abroad. With E. D. Cope's death in 1897 and the appointment of R. P. Bigelow as editor, there was no longer a discipline distinction in the journal. The character of the articles was mixed, although descriptive studies predominated. Science, the publication of the American Association for the Advancement of Science, offered a similar picture of American biology. The early editions revealed an interest in natural history, evolution, medicine and technology. By the mid-1890's articles began to appear that noted the major problems of cell development and embryology, but even at this time the journal appeared to be very broad in scope. By 1900, the biological articles in Science represented the range of research that was characteristic of this period.

The only journal that made an overt departure in the direction of the new emphasis for experimental work was the Journal of Experimental Zoology. Interestingly enough, it was founded by a nucleus of Brooks's students, published in Baltimore and included Brooks on the editorial board.[80] Even in this journal, there was not a clear break between studies that were experimental and those that were descriptive. The majority of the articles did emphasize the application of the new experimental techniques to questions of regeneration, cell regulation, self fertilization, blastomere separation, etc. But almost every volume included a smattering of pure morphology.[81]

The foregoing description of the mutual dependence and relatedness of experimental studies and morphological studies, the rise of sub-disciplines in biology during the 1890's and the continuation of morphological research into the twentieth century through evidence from journals, reveals that the development of American biology at the end of the nineteenth century cannot be pictured as a simplistic emergence of experimental biology. The state of the art was much more complicated. To understand the changes that did take place in the 1890's, the historian must consider the fundamental changes that took place in the questions biologists were asking.

The work in American biology from 1860-1890 was basically directed toward providing information that could be used to demonstrate the authenticity of the biogenetic law and the genealogical relationships that existed in the animal world. Morphology became the major enterprise addressing these questions. The program enjoyed much early success through the discovery of ancestral forms and the elucidation of an invertebrate ancestry for the vertebrates. Despite these successes, by the 1880's problems were emerging at the foundation of the research program. In the case of Brooks, he maintained a successful morphological approach by adopting a more sophisticated criterion for homologies and by eliminating the search for an universal ancestral form.

The problems that were uncovered in the eighties eventually became so paramount that the morphologists in the 1890's adopted a new foundation for their work. Cell lineage work replaced germ layer homologies and phylogenetic "indications" replaced ancestral genealogies. The emphasis was displaced from phylogeny and placed upon ontogenetic development. While the investigators did not ignore probable applications from their research to phylogenetic considerations, the research questions tended to examine only the actual developmental events. Observations upon these events were soon supplemented by research programs that asked questions concerning the causal explanations for the observed phenomena.

The result of the change from ontogenetic and phylogenetic questions to investigations stressing ontogeny was a change in methods. To the observational and descriptive embryological morphology of the 1880's was supplemented the experimental techniques of the 1890's. Consequently, one observed the development of experimental embryology as an application of the methods of physiology to embryological morphology. The new experimental program did not replace the morphological one. Instead, it was able to ask questions of a causal nature that the descriptive methodology could not. Furthermore, the experimentalist was able to frame the questions in such a manner that they could be tested experimentally. Nevertheless, as E. B. Wilson pointed out, this new program in biology depended heavily upon the "very framework" of embryological morphology.

In terms of this assessment of American biology, where does W. K. Brooks fit? It is the contention of this study that Brooks must be considered as an important figure in the development of American biology. As America's major morphologist in the 1880's, Brooks dealt with the major problems in morphology, he conducted impressive research in descriptive embryology and invertebrate zoology, and he provided the primary instruction for many of America's most notable biologists. Considered in this light, Brooks must be seen as representing the initial stage for the emergence of the sophisticated biological community that came to characterize the situation in America. To Brooks's morphological base was added the experimental embryology work of Roux and Driesch and the physiological morphology of Loeb and Morgan. These influences became thoroughly intertwined in the 1890's in the United States to produce a plethora of research programs, new sub-disciplines, new methodologies and new questions.

NOTES

CHAPTER FIVE

1. W. K. Brooks, Foundations of Zoology (New York: The Macmillan Company, 1899).

2. David Starr Jordan, "A Sage in Science," Science 9 (1899), p. 532.

3. W. K. Brooks, Foundations of Zoology, pp. 140-141.

4. The journal, published in Boston, was initially dependent upon the generous support of Edward Phelps Allis, Jr. (a wealthy industrialist). Allis also underwrote the Lake Laboratory in Milwaukee, Wisconsin where Whitman had been director.

5. C. O. Whitman, "Editor's Note," Journal of Morphology 1 (1887), p. ii.

6. J. W. Jenkinson, Experimental Embryology (Oxford: At the Clarendon Press, 1909), p. 12.

7. Edmund B. Wilson, "The Mosaic Theory," in Biological Lectures Delivered at the Marine Biological Laboratory of Wood's Holl, 1893 (Boston: Ginn and Company, 1894), p. 1.

8. Ibid., p. 2.

9. Edmund B. Wilson, "The Embryological Criterion of Homology," in Biological Lectures Delivered at the Marine Biological Laboratory of Wood's Holl, 1894 (Boston: Ginn and Company, 1895), pp. 103-104.

10. Edmund B. Wilson, "Aims and Methods of Study in Natural History," Science 13 (1901), p. 17.

11. One of the earliest experiments on embryonic development was the study of the effect of gravity upon cleavage by E. Pflüger, "Ueber den Einfluss der Schwerkraft auf die Theilung der Zellen," Archiv für Physiologie 31 (1883), pp. 311-318. The article was read widely and referred to through the 1880's.

12. Edmund B. Wilson, "The Mosaic Theory," p. 3.

13. Graduates were awarded degrees in "Zoology" (Brooks) or in "Animal Physiology" (Martin).

14. It is important to realize the distinction between physiology and experimentation. Prior to the 1880's and 1890's physiology was the main branch of biology into which the application of experimental methods was applied. Morphology, particularly the aspect of it which was concerned primarily with developmental studies, did not involve any of this work. Toward the end of the nineteenth century, the techniques the physiologists used were applied to specific problems in embryology. Although it was the experimental method of physiology that was borrowed by the embryologists, many investigators referred to the change in the studies as the application of physiology to embryology or morphology. In reality, the change was the use of the experimental methods to studies that had been restricted to descriptive methods.

15. E. A. Andrews, "Experimental Embryology," American Naturalist 26 (1892), p. 367.

16. Ibid., pp. 367-382, 580-592. The major articles of all these experimentalists were briefly described in this reference. In this way, the American scientist became familiar with themes discussed at Naples.

17. Ibid., p. 371. Roux's research was widely published in many of Germany's leading scientific journals. Andrews refers to the major articles.

18. Edmund B. Wilson, "The Mosaic Theory," p. 8.

19. Driesch's early work is contained in "Entwicklungsmechanische Studien. I. Der Werth der beiden ersten Furchungs-zellen in der Echinodermenentwicklung. II. Üeber die Beziehung des Lichtes zur ersten Etage der Theirischen Formanbildung," Zeitschrift für Wissenschaft Zoologie 53 (1891), pp. 160-183.

20. Other major figures in American biology who attended sessions at Naples became important in the establishment of the Marine Biological Laboratory. These included C. O. Whitman, W. M. Wheeler (1865-1937), Julia Platt (n.d.), Ida Hyde (1863- ?), H. S. Jennings, Nettie Stevens, C. M. Child, C. B. Davenport (1866-1944) and R. S. Lillie. (Donna Jeanne Haraway, "The Marine Biological Laboratory at Woods Hole: An Ideology of Biological Expansion [unpublished paper, Johns Hopkins University], p. 7.)

21. For good treatments of the developments leading to the establishment of the Marine Biological Laboratory, see Donna Jeanne Haraway, "The Marine Biological Laboratory at Woods

Hole" and Frank R. Lillie, The Woods Hole Marine Biological Laboratory (Chicago: University of Chicago Press, 1944).

22. C. O. Whitman, "First Annual Report," Marine Biological Laboratory Annual Reports 1 (1888), p. 16.

23. This is not to say that Woods Hole was intended only as a morphological research facility. Physiologists noted the possible value of the MBL for their own work. W. T. Sedgwick (1855-1921), a physiologist who obtained his graduate training at Johns Hopkins and who had done some graduate work under Brooks, observed:

> The opening of the New Marine Biological Laboratory at Wood's Holl, Mass., is an event of more than ordinary importance to physiologists--not so much for what it now is, as for what it promises to be. At present it is devoted chiefly to the study of morphological problems, owing to the pressing demands from morphologists for opportunities for sea-side work, but even now physiologists find themselves heartily welcomed, and in the numerous problems offered by the muscle and nerve physiology of star fishes, jelly fish, sea-urchins and the like; in the question of phosphorescence; in rudimentary sense organs; in reproduction at its simplest; and in a host of still broader questions concerning the physiology of protoplasm, they will find abundant material for prolonged and absorbing study. The famous zoological station at Naples has lately taken steps toward offering opportunities to physiologists equal to those which it has for years supplied to morphologists; and it cannot be doubted that equally brilliant results will follow and will enrich physiology, as morphology as already been enriched. No special facilities have as yet been provided for physiologists at Wood's Holl, but it is the desire and the intention of the trustees to make the laboratory, in fact as well as in name, a Biological laboratory.

(W. T. Sedgwick, "Physiology," American Naturalist 22 [1888], p. 756.) Statements like Sedgwick's reveal the split between morphology and physiology that existed prior to the 1890's (see Note 14).

24. Edmund B. Wilson, "The Embryological Criterion . . .," p. 124.

25. Ibid., p. 123.

26. C. O. Whitman, "Some of the Functions and Features of a Biological Station," in Biological Lectures Delivered at the Marine Biological Laboratory of Wood's Holl, 1896-1897 (Boston: Ginn and Company, 1898), p. 240.

27. One of the major points of this study is that Brooks had a profound impact upon many students who went on to become important figures in American science. Although the nature of this influence cannot be determined with exactness, there are innumerable areas in which Brooks could have influenced his students. Certainly the several references by Dennis M. McCullough, "W. K. Brooks's Role in the History of American Biology," Journal of the History of Biology 2 (1969), pp. 411-438, negating Brooks's influence cannot be accepted. His major position is mirrored in the following:

> However, both the anti-experimental and morphological biases of William Keith Brooks detract from the positive influence which he was able to exert on his students. Brooks failed to perceive the new directions in which biology was moving, and, consequently, the scientific problems on which his students worked while at Hopkins were to be of minor significance in the oncoming experimental era. (p. 432)
>
> . . . But the fact remains that none of his best students followed Brooks's own line of investigation or his own method of research. . . . This study suggests that his influence was less important in terms of setting a direction for research than has previously been believed. . . . This paper has tried to show that, in terms of available evidence, Brooks does not seem to have had the profound influence on early twentieth-century biology that some historians have claimed. (p. 438)

The main points of this study dispute these conclusions.

A more accurate appraisal was alluded to by Donna Jeanne Haraway, Crystals, Fabrics, and Fields (New Haven and London: Yale University Press, 1976).

> That Harrison, Wilson, Conklin and other American experimental embryologists were all students of W. K. Brooks at Johns Hopkins was surely important to their shared concerns. (p. 36)

28. S. F. Clarke (1897-1921), E. G. Conklin (1897-1952), H. H. Donaldson (1912-1938), Caswell Grave (1920-1943), Ross G. Harrison (1908-1959), George Lefevre (1909-1923), M. M. Metcalf (1897-1940), T. H. Morgan (1897-1947), H. F. Osborn (1890-1902), W. T. Sedgwick (1897-1900) and E. B. Wilson (1890-1924). From C. D. Seligson, "The Chesapeake Zoological Laboratory, 1878-1906" (unpublished manuscript, Johns Hopkins University, 1975).

29. E. G. Conklin, "Address at the Jubilee of the Department of Biology at Case Western Reserve University" (1938), Princeton University, Firestone Library Manuscript Room, E. G. Conklin Papers.

30. Cell lineage work was pioneered and developed at Johns Hopkins University (CZL) and the MBL by Wilson, Conklin and Whitman. It is interesting to note that the descriptive studies, so important to work of an experimental nature, preceded the rise of experimentalism at the MBL. From 1888-1893, cell mapping research predominated. After 1893, work from the Entwicklungsmechanik program supplemented these descriptive studies.

31. E. G. Conklin, "The Embryology of Crepidula, a Contribution to the Cell Lineage and Early Development of Some Marine Gasteropods," Journal of Morphology 13 (1897), pp. 1-205.

32. E. Newton Harvey, "Edwin Grant Conklin," National Academy of Science Biographical Memoir 31 (1958), p. 63.

33. Ibid.

34. Edmund B. Wilson, "Cell Lineage and Ancestral Reminiscence," in Biological Lectures Delivered at the Marine Biological Laboratory of Wood's Holl, 1898 (Boston: Ginn and Company, 1899), p. 26.

35. Donna Jeanne Haraway, Crystals, Fabrics, and Fields, p. 88.

36. E. G. Conklin, "Protoplasmic Movement as a Factor of Differentiation," in Biological Lectures Delivered at the Marine Biological Laboratory of Wood's Holl, 1898 (Boston: Ginn and Company, 1899), pp. 73, 90.

37. Edmund B. Wilson, "Cell Lineage and Ancestral . . .," p. 21.

38. W. K. Brooks, "Are Heredity and Variation Facts?" Advance print from Seventh International Zoological Congress, Boston meeting, August 19-24, 1907 (Cambridge, Mass.: 1909), p. 42.

39. Edmund B. Wilson, "Cell Lineage and Ancestral . . .," pp. 21-22.

40. E. G. Conklin, "The Embryology of Crepidula," pp. 4-5.

41. E. G. Conklin, "Cleavage and Differentiation," in Biological Lectures Delivered at the Marine Biological Laboratory of Wood's Holl, 1896-1897 (Boston: Ginn and Company, 1898), pp. 17-18.

42. Edmund B. Wilson, "The Structure of Protoplasm," in Biological Lectures Delivered at the Marine Biological Laboratory of Wood's Holl, 1898 (Boston: Ginn and Company, 1899), p. 2.

43. Letter, W. K. Brooks to D. C. Gilman, June 18, 1881, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

44. W. K. Brooks, Foundation of Zoology, p. 9.

45. Ph.D. awarded in 1905 as "Embryology of Turritopsis nutricula." Published as: W. K. Brooks and Samuel Rittenhouse, "On Turritopsis nutricula," Boston Society of Natural History Proceedings 33 (1907), pp. 429-460.

46. Ibid., p. 40.

47. W. K. Brooks, "Are Heredity and Variation Facts?" p. 42.

48. T. H. Morgan, "Edmund Beecher Wilson (1856-1939)," Biographical Memoirs of the National Academy of Science 21 (1941), pp. 315-342.

49. "William Keith Brooks. A Sketch of His Life by Some of His Former Pupils and Associates," Journal of Experimental Zoology 9 (1910), p. 5.

50. Ibid., pp. 6-7.

51. E. G. Conklin, "The Century's Progress in Biology." Address at Vassar College (1901). Princeton University, Firestone Library Manuscript Room, E. G. Conklin Papers.

52. Letter, W. K. Brooks to D. C. Gilman, July 15, 1885, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

53. Letter, H. W. Conn to D. C. Gilman, July 3, 1884, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

54. Letter, H. W. Conn to D. C. Gilman, July 26, 1884, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

56. William Bateson, "Evolutionary Faith and Modern Doubts," Science 55 (1922), p. 55.

57. Letter, Joseph LeConte to W. K. Brooks, April 9, 1887, Johns Hopkins University, Eisenhower Library Manuscript Room, Brooks file.

58. Donna Jeanne Haraway, "The Marine Biological Laboratory . . .," p. 17.

59. Letter, W. T. Sedgwick to D. C. Gilman, July 12, 1888, Johns Hopkins University, Eisenhower Library Manuscript Room, Gilman collection.

60. "In Memory of William Keith Brooks" (Dinner memorial, December 31, 1908). Personal property of Amasa B. Ford, M.D., Chagrin Falls, Ohio.

61. Dennis M. McCullough, "W. K. Brooks's Role in the History of American Biology," provides such a characterization.

62. William Coleman, Biology in the Nineteenth Century: Problems of Form, Function and Transformation (New York: John Wiley & Sons, 1971) and Garland E. Allen, Life Sciences in the Twentieth Century (New York: John Wiley & Sons, 1975) both develop a similar pro-experimental thesis. Allen's latest work, Thomas Hunt Morgan: The Man and His Science (Princeton, New Jersey: Princeton University Press, 1978) is written in this same genre.

63. J. P. McMurrich, "Cell Division and Development," in Biological Lectures Delivered at the Marine Biological Laboratory of Wood's Holl, 1894 (Boston: Ginn and Company, 1895), p. 175.

64. E. G. Conklin, "The Marine Biological Laboratory," Science 11 (1900), p. 340.

65. Examples of articles in Journal of Morphology: T. H. Morgan, "The Origins of the Test-Cells of Ascidians" (1891); Edmund B. Wilson, "The Cell Lineage of Nereis" (1892); J. P. McMurrich, "Embryology of the Isopod Crustacea" (1895); E. G. Conklin, "The Embryology of Crepidula" (1897); H. McE. Knower, "The Embryology of a Termite" (1899); F. R. Lillie, "The Organization of the Egg of Unio. Based on a Study of its Maturation, Fertilization and Cleavage" (1901); N. Yatsu, "Observations on Ookinesis in Cerebratulus laeteus (Verrill)" (1909).

66. Neohide Yatsu, "Observations on Ookinesis in Cerebratulus laeteus (Verrill)," Journal of Morphology 20 (1909), p. 354.

67. Howard Edwin Enders, "A Study of the Life-history and Habits of Chaetopterus variopedatus (Renier et Claparede)," Journal of Morphology 20 (1909), p. 480.

68. E. G. Conklin, "Cleavage and Differentiation," pp. 41-42.

69. Edmund B. Wilson, "Cell Lineage and Ancestral . . .," p. 41.

70. Ibid., p. 42.

71. E. G. Conklin, "The Mutation Theory from the Standpoint of Cytology," Science 21 (1905), p. 528.

72. Ibid., pp. 528-529.

73. T. H. Morgan, "Developmental Mechanics," Science 7 (1898), p. 156.

74. Ibid.

75. Ibid., pp. 156-157.

76. As has been cited in notes 14 and 23, many biologists prior to the 1890's viewed biology as split into morphology and physiology. With the increasing application of experimental techniques from physiology to morphology, several of the biologists viewed biology as undergoing a fusion of these two approaches. R. P. Bigelow, the editor of American Naturalist and a graduate student of Brooks, noted the extensive overlap between physiology and morphology in 1898.

> Generally speaking, the obvious facts of natural science have been discovered, and investigation is trending away from them toward the deeper, more remote and more fundamental phenomena. Students following these deeper lines of research sooner or later find themselves on the border where their scientific field borders their neighbor's. The morphologist who seeks to explain the causes of development soon finds himself involved in questions of physiology. Physiologists, on the other hand, in studying the functions of the nervous system, for example, have found it possible to draw important conclusions from data furnished by morphology.

(R. P. Bigelow, "The Aim of the American Naturalist," American Naturalist 32 [1898], p. 50). While this overlap is not the subject of this study, it is of interest to note that a biologist of Bigelow's stature saw morphology and physiology as becoming increasingly complementary. A similar situation existed between descriptive studies and experimental studies.

77. Edmund B. Wilson, "Aims and Methods of the Study . . .," p. 20.

78. Ibid., p. 21.

79. A later examination of the major journals will illustrate the widespread nature of morphological studies at this time.

80. The editorial board consisted of Brooks, W. E. Castle, Conklin, C. B. Davenport, H. S. Jennings, F. R. Lillie, J. Loeb, Morgan, G. H. Parker, Whitman, Wilson and Harrison.

81. Examples of descriptive work in Journal of Experimental Zoology: C. B. Davenport and Marian E. Hubbard, "Studies in Evolution of Pecten" (1904); H. M. Stevens, "A Study of the Germ Cells of Aphis rosae and Aphis venotherae" (1905); Florence Pebbles, "The Location of the Chick Embryo upon the Blastoderm" (1904); Louis H. Greger, "Observations on the Life History of Tillira magna" (1909); Samuel Rittenhouse, "The Embryology of Stomotoca apicata" (1910); and D. S. Johnson, "Studies in the Development of the Piperaceae" (1910).

EPILOGUE

The stated purpose of this study was to examine the development of descriptive embryology between 1875-1900 by conducting a detailed inspection of the work of William Keith Brooks. The preceding examination has provided the necessary information to allow a better understanding of late nineteenth-century American morphology and to obtain a reliable interpretation concerning the relationship of this morphological program to experimental studies.

The work of Brooks, as America's foremost morphologist, demonstrated that the descriptive investigator dealt with more than merely speculative ancestries. The program of evolutionary reconstruction underwent gradual modifications from 1860-1900 in order to provide a more accurate basis for the real relatedness of organisms. The early work received its impetus from the biogenetic law and the theory of species descent. It was also widely accepted that relationships between species could best be discovered through embryological work. The result was the maturation of descriptive embryology, emphasizing developmental studies and life histories of organisms. While Brooks's own research was always in this tradition, problems with evolutionary reconstruction led to refinements in technique and method.

The early preference for uncovering homological relationships between organisms raised the question as to what method should be used to determine homologies. Was comparative anatomy adequate or should a more precise embryological criterion be utilized? Brooks opted for an embryological basis. However, continued developmental work in the 1880's concerning the supposed homology of the primitive germ layers revealed grave problems. No longer could the primitive gastraea be considered as the universal ancestor and, as a result, the basis for homologies was brought into doubt. Research turned from the gastrula to the unsegmented egg, and the subsequent study of its development. The major question became, did the mode of germ layer origin reveal evolutionary heritage or was the fate of the germ layers more important? To address these questions effectively, cell lineage was implemented and applied to development. This work served to be important in providing a sophisticated basis for embryology and in leading to investigations of a more experimental nature.

This study does not maintain that there was a simple causal relation leading from the morphological work to the experimental programs. Indeed, the two approaches to embryological investigation shared much in common. At the same time, it has been suggested that many of the questions uncovered by the descriptive studies became important for the experimental investigations. As more attention became focused upon ontogenetic events, these phenomena come to be considered apart from phylogeny. In the 1890's this led to questions such as why does ontogeny occur, or what are the forces that produce ontogenetic change, or how does the simple cell differentiate with such precision? To address these questions, the descriptive methodology had to be supplemented with experimental tools.

As has been previously demonstrated, biological investigators at the end of the nineteenth century recognized the shared concerns and problems of morphology and experimental biology. Even Wilhelm Roux, the founder of *Entwicklungsmechanik* noted this characteristic.

> Thus phylogenetic and ontogenetic developmental mechanics receive from the older branches of biology besides their problems much causal information, and still more guidance to such information. *The methods with which this knowledge has been acquired will continue to be necessary to developmental mechanics even in the future*, still many causal problems are scarcely accessible to experimental investigation, and since, moreover, the correct interpretation of the results of experiment is often frought with such difficulty, that every possible aid from other sources must be utilized.[1]

Roux considered developmental mechanics to be very much dependent upon any kind of biological information, descriptive or experimental. Although the wholesale speculations upon phylogeny that were characteristic of the early work may have been discarded by the end of the nineteenth century, investigators in the 1890's realized the value of a more limited phylogenetic program.

The experimental work never replaced the descriptive studies. From examinations of scientific journals at the end of the nineteenth century and the beginning of the twentieth century, there is evidence that morphological work flourished in the United States during this period. This was particularly true of descriptive studies in embryology for they had an important application to the new work from Entwicklungsmechanik. Cell mapping studies, especially at the MBL, became a standard initial phase in more experimental investigations. This embryological work was also of value for its own sake. Studies of development and life history provided the essential information for the determination of taxonomic classification. The same value of the descriptive work for biology is currently recognized.

> Many of our assumptions about animal phylogeny are based upon embryology. The various hypotheses concerning the origins of various higher taxa and their relationships to one another depend a great deal on the evolution of ontogenies. Our views about the major evolutionary lines within the animal kingdom are established on developmental features. Even with the knowledge we now possess it seems obvious to me that these ideas . . . are in need of major re-thinking; but again we need additional basic information.[2]

Therefore descriptive embryology not only contributed to experimental studies, but it also yielded valuable information of its own. As E. B. Wilson noted, these studies provided the "very framework" for all of biology.[3]

It is more instructive to consider the 1890's as a period in which experimental methods applied to biological studies that had been previously descriptive, resulted in a proliferation of biological specialties in the United States. In examining embryology from 1860-1900, such an appraisal is quite accurate. While prior to 1890, most morphological work was in descriptive embryology, developments in the 1890's changed their character dramatically. By the beginning of the twentieth century, comparative embryology, experimental embryology and physiological embryology were well established. The situation, therefore, cannot be legitimately described as a simplistic break from a descriptive tradition to an experimental tradition or as a dichotomy between morphological work and physiological work.

By obtaining a better understanding of the complexity of biological developments at the end of the nineteenth century, it is hoped that a better understanding of Brooks's role in the development of American biology will result. Brooks's research at various marine laboratories contributed much valuable information for life histories that later work could draw upon. It is noteworthy to point out that the most well known of Brooks's students (Wilson, Harrison, Conklin, Morgan and Andrews) all spent several summers of investigation with Brooks at the CZL. Several men, at Brooks's urging, also spent time at other marine stations.

On an institutional level, Brooks's emphasis upon investigations involving marine organisms provided a major impetus to the development of marine laboratories in the United States. The CZL became an important training ground for zoologists in the United States and also served to influence the development of other marine programs. In addition, Brooks's position as an original faculty member in the first graduate program in the United States made him a pivotal figure in the development of American biology. Through the instruction he offered at Johns Hopkins University and the CZL, Brooks trained a whole generation of leading American biologists.

Although the exact nature of the scientific work some of Brooks's students conducted after leaving Johns Hopkins was experimental this should not be necessarily interpreted as marking a distinct break from the purely morphological tradition of Brooks. Nor should this be interpreted as indicating that Brooks had little influence upon these students. Certainly, as Donne Jeanne Haraway stated[4] and as evidence in Chapter Five indicated, the shared concerns of Brooks and his students provide evidence for some kind of influence. Often this kind of impact of a mentor on a student is most difficult to establish. However, that a recognized authority in biology like Brooks, had an impact upon creating a wider orientation, providing norms and standards, inculcating values and attitudes and imparting behavior patterns to his students, seems undeniable. Even if the substantive nature of the work underwent a change, the contact between teacher and student was beneficial.

> It's the contact: seeing how they operate, how they think, how they go about things. [Not the specific knowledge?] Not at all. It's learning a style of thinking, I guess. Certainly not the specific knowledge.[5]

Many of Brooks's students, while often noting differences between the exact nature of their work and Brooks's work, provided ample evidence for influence of this nature.[6]

It is important to note that Brooks's role as a first-rate scientist was not his only influence. By creating an ambience conducive to important scientific work, Brooks made the CZL and the Biological Laboratory at Johns Hopkins important training sites for future scientists. Such "evocative environments" provided a situation in which good scientific investigation proliferated as a result of the mentor and the graduate students working as "co-workers."[7]

Future investigations need to be directed at the relationship between morphology and experimental biology by examining students trained by Brooks but practicing under a more experimental program. The present study has described the morphology program in the late nineteenth century that served to educate many of the important American biologists. The study has also called for an interpretation that stresses the complementarity of morphology and experimental biology. To demonstrate clearly the complementary nature of this relationship, detailed studies of the change in questions and methods between the work of Brooks and his students need to be conducted. Work in this direction promises to yield a better understanding of the important contributions of morphology and experimental biology in the history of the development in the life sciences.

NOTES

EPILOGUE

1. Wilhelm Roux, "The Problems, Methods and Scope of Developmental Mechanics," trans. by W. M. Wheeler, in Biological Lectures Delivered at the Marine Biological Laboratory of Wood's Holl, 1893 (Boston: Ginn and Company, 1894), pp. 173-174.

2. Gary J. Brusca, General Patterns of Invertebrate Development (Eureka, Calif.: Mad River Press, Inc., 1975), p. 1.

3. Edmund B. Wilson, "The Embryological Criterion of Homology," in Biological Lectures Delivered at the Marine Biological Laboratory of Wood's Holl, 1894 (Boston: Ginn and Company, 1895), p. 125.

4. Donna Jeanne Haraway, Crystals, Fabrics, and Fields (New Haven and London: Yale University Press, 1976), p. 123.

5. Harriet Zuckerman, Scientific Elite: Nobel Laureates in the United States (New York: The Free Press, 1977). Zuckerman interviewed many American Nobel Laureates concerning their relation to their mentor. All agreed that even though they received little substantive knowledge from their master, they did learn the style of scientific work, conceptions of the role of the working scientist and methods of approaching problems or asking provocative questions. Certainly this is an important role that can be applied to Brooks's role at Johns Hopkins. (Morgan won the Nobel prize in 1933 and Harrison was nominated for the award.)

6. See Chapter Five.

7. Harriet Zuckerman, Scientific Elite, pp. 131, 172.

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