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Benjamin Harrison Grave: American Marine Invertebrate Zoologist

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1. Introduction

Benjamin Harrison Grave (1878-1949) (Figure 1) was an American zoologist and educator. A native of Indiana, he left the family farm for graduate study in zoology at Johns Hopkins University and went on to a distinguished career in teaching and research. He published 23 articles on marine invertebrates that included observations on 20 species ranging over 7 phyla. These studies focused primarily on anatomy, gamete and fertilization biology, embryology, and general aspects of life history. He is best known for his articles on the marine invertebrates in the vicinity of Woods Hole, Massachusetts, and Beaufort, North Carolina. His teaching career (1904-1942) encompassed a broad range of biological topics, in the laboratory and in the field, primarily addressed to undergraduates. He was a life-long Quaker known for his passion for justice and love of nature.

2. Origins and Early Years

Benjamin Harrison Grave was born on December 5, 1878, in Monrovia, Indiana, the second son of Thomas Clarkson Grave (1840-1924) and Anna Hubbard Grave (1848-1908).¹ Benjamin Grave's life came to a close in January 1949 only 40 km from Monrovia in Indianapolis, Indiana, from complications following a fall. Though his career and



Figure 1. B.H. Grave at the microscope, 1926 (Courtesy of the Marine Biological Laboratory Archives, <http://hpsrepository.asu.edu/handle/10776/2870>)

education would lead him across the United States, the greater part of his years were spent within 200 km of Monrovia.

Grave was a “birth-right Quaker”, meaning that he was born into a family who belonged to the Society of Friends, commonly known as the Quakers. Benjamin’s father was descended from Thomas Grave, an English Quaker who emigrated and settled in New Castle County, Delaware, in 1691.² Both the Grave and Hubbard families moved from Pennsylvania to Indiana in the early nineteenth century, part of a “great migration” of Quakers to what is now the American mid-west.³

Benjamin’s great-grandparents, Enos (ca. 1771-1842) and Elizabeth Jones Grave (1775-ca. 1860), reached Indiana in 1816, settling in Wayne

County, Indiana, north of Richmond, and joining the Whitewater Monthly Meeting.⁴ Benjamin’s grandfather, David Isaac Grave (1803-1864), was born in Brownsville, Pennsylvania. After moving west with his family, he became a coverlet weaver, inventing his own jacquard loom.⁵ Some of his work survives in the collection of the Art Institute of Chicago.⁶ After both David Isaac and his wife, Elizabeth Hartley Grave, were dismissed from the Whitewater Monthly Meeting for nonconformity,⁷ they and their children moved to Monrovia, Indiana, in 1850. David’s son, Thomas Clarkson Grave, remained in Monrovia as a farmer, married Anna Hubbard in 1868, and raised his family there.⁸

Monrovia, a farming community in central Indiana, began as an enclave of Friends, and the West Union Friends Meeting, established in 1832, was the center of the Monrovia community. The Meetinghouse was the town’s first religious building and school. Both of Benjamin Grave’s parents, and all four of his grandparents, are buried in the West Union Cemetery adjacent to the meetinghouse. West Union Friends Meeting is still active; it is affiliated with the Friends United Meeting, which is headquartered in Richmond,

Figure 2. Joseph Moore (Courtesy of Earlham College Archives)

Indiana.⁹

Benjamin Grave left Monrovia to attend Friends Central Academy in Plainfield, Indiana, from 1895-1898. He then earned a B.S. degree in Biology from Earlham College in Richmond, Indiana, a Quaker-affiliated college. It is possible, perhaps likely, that he did not interact with non-Quakers until he had graduated from college.

Benjamin Harrison Grave grew up with three brothers: Caswell (1870-1944), Thomas Hubbard (1880-1961), and Everette Floyd, known as Floyd (1885-1951). All were well educated for their day, completing B.S. degrees: Caswell graduated from Earlham College in 1895, Benjamin in 1903, and Thomas in 1906; Floyd graduated from Carleton College in Northfield, Minnesota, in 1908. Caswell and Benjamin went on to complete Ph.D.'s and pursue careers as invertebrate zoologists, Floyd became a medical doctor. Only Thomas stayed in agriculture, becoming a rancher in Gresham, Oregon.¹⁰



3. College and Graduate Study

Grave was a student at Earlham College, Richmond, Indiana, for five years, graduating with a B.S. degree in 1903. He followed a broad liberal arts program with in-depth study in biology, and other courses including geology, physics, chemistry, history, and French and German languages.¹¹ His scientific influences at Earlham were Professor David Worth Dennis (1849-1916),¹² who taught biology and chemistry, and Professor Joseph Moore (1832-1905) (Figure 2),¹³ who taught biology and geology. Grave was heavily involved with college athletics, competing on behalf of Earlham on their track, baseball, and football teams (Figure 3). He held the Indiana state record for the quarter mile for three years.¹⁴ During his student years in Richmond, Grave met his future wife Lucile H. Moore (1879-1968), Earlham class of 1902 and daughter of Joseph Moore. Benjamin's younger brother Thomas was also on campus then, graduating with the class of 1906.

After graduating from Earlham College in 1903, Grave started graduate study in biology at Johns Hopkins University, completing his Ph.D. there in 1910. It was anything



Figure 3. B.H. Grave, student athlete
(Courtesy of Earlham College Archives)

but a direct path from start to finish, however. In his initial application to Johns Hopkins, he stated that he would like to study both botany and zoology.¹⁵ After the 1903-1904 academic year, he spent the summer at the Biological Laboratory at Cold Spring Harbor, New York, which was then affiliated with the Brooklyn Institute of Arts and Sciences. Grave studied both comparative anatomy (principally of invertebrates) there, under Henry Sherring Pratt, and botany with Forrest Shreve of Johns Hopkins.¹⁶ In the fall of 1904, instead of returning to Johns Hopkins, Grave left for Carleton College in Northfield, Minnesota, where his brother Floyd was a student. During the summer of 1905, he studied at the University of Chicago, enrolling in four courses: three in botany and one in biblical history (The

History of the Priest System, offered by the Department of Semitic Languages and Literatures). He earned credit for his work in Elementary Plant Physiology and General Morphology of Spermatophytes, but did not complete Methods in Plant Histology.¹⁷ For Grave, the highlight of the summer was studying with Professor John Merle Coulter, his instructor in the spermatophytes course.¹⁸

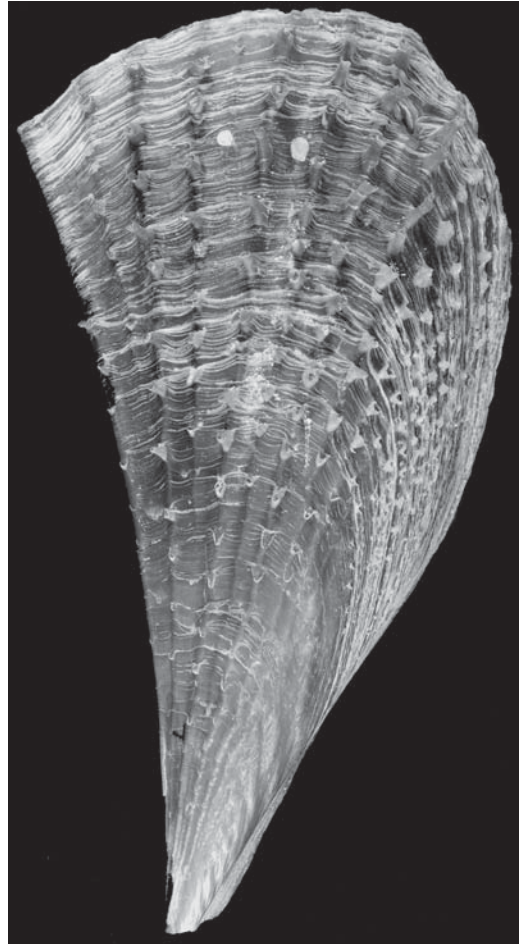
Grave completed a Master of Science degree in Botany at Carleton in 1906, with a thesis on *Lilium tigrinum*.¹⁹ In the spring of 1906, he reapplied to continue his studies at Johns Hopkins and was readmitted.²⁰ Having resumed his studies at Johns Hopkins, he also was a member of the track team there in the 1906-07 academic year.²¹

Grave's dissertation²² was an anatomical study of the bivalve mollusk, *Atrina rigida* (Lightfoot, 1786), a member of the Pinnidae (Figure 4). According to Grave, the species ranged in distribution in the western Atlantic from northern regions of South America to Cape Hatteras in North Carolina. The largest specimen found by Grave was 14 x 9 x 3 inches. Individuals live in shallow water and are occasionally exposed at low tide. They burrow in the soft substrate, anterior end pointed downward, and attach to solid objects using an extensive byssus apparatus. *Atrina rigida* is a species that was of economic consequence in the nineteenth and early twentieth centuries. It has a large posterior adductor muscle that is edible. Grave estimated that about 20% of specimens he examined contained black pearls; when present, Grave found as many as 10 pearls in a single

Figure 4. Left valve of *Atrina rigida* (MCZ Mollusk Collection Lot 216963)

specimen. Finally, the byssus, being well developed, was used in manufacturing articles such as shawls, waistcoats, gloves, caps, and purses.

Its common abundance, lack of prior study, and economic utility provided the rationale for a baseline study of the anatomy of this species and made for an excellent dissertation subject in Grave's era. Grave credits William Keith Brooks (1848-1908) (Figure 5) with the suggestion he pursue this topic. Brooks was professor of biology at Johns Hopkins University from 1891-1908.²³ His journey into marine biology began with studying under Louis Agassiz and spending two summers (1873 and 1874) at the Penikese Island laboratory in Buzzards Bay, Massachusetts. In 1875, Brooks investigated the embryology of salps at Alexander Agassiz's laboratory in Newport, Rhode Island. Brooks received his doctoral degree from Harvard University in 1875. At Johns Hopkins University, Brooks founded the Chesapeake Zoology Laboratory in 1878, which he directed for many years. Although Brooks published extensively on a wide diversity of marine invertebrates, it was the oyster that most captured his zeal. His commitment to farming over fishing placed him in the middle of a major controversy in the Chesapeake community.²⁴ To this end, Brooks published in 1891 a popular book on oysters and the prospects of culturing to restore the oyster industry in Maryland.²⁵ A second edition was published in 1905. Brooks's legacy in biology extends well beyond his own researches as he mentored some students who went on to become among the most influential biologists of their day including: E. G. Conklin, R. C. Harrison, T. H. Morgan, and E. B. Wilson.²⁶



Although Brooks is credited with steering Grave toward the study on *Atrina rigida* he died in 1908 and Grave's dissertation was not published until 1911. The research was supervised by Professor Ethan Allen Andrews (1859-1956) (Figure 6). Andrews had been an undergraduate at Yale and graduate student at Johns Hopkins.²⁷ He received his Ph.D. in 1887 with a dissertation on polychaete annelids of Beaufort, North Carolina.²⁸ Andrews



Figure 5. William Keith Brooks (courtesy of Ferdinand Hamburger Archives, Sheridan Libraries, Johns Hopkins University)

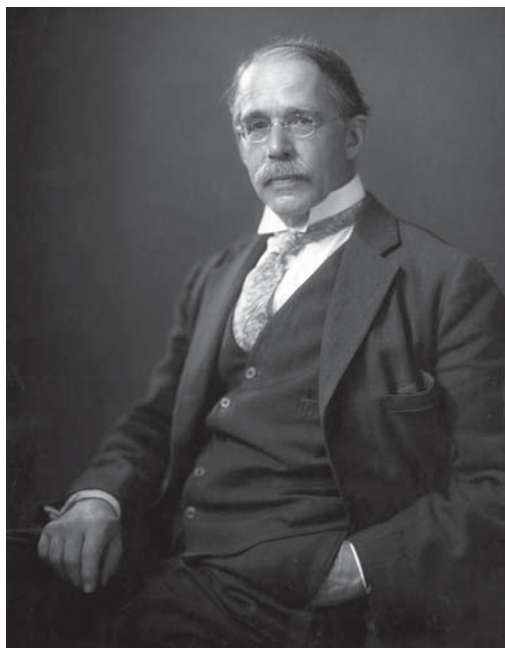


Figure 6. Ethan Allen Andrews (courtesy of Ferdinand Hamburger Archives, Sheridan Libraries, Johns Hopkins University)

joined the faculty at Johns Hopkins in 1887 and became a full professor in 1908.²⁹ Andrews, like Brooks, had broad interests and published numerous papers over a range of organisms, including protozoans (especially folliculinids), numerous invertebrates, insects, and several papers on vertebrates, including one on a whale skeleton. Unfortunately, we found no further information about his relationship with Grave.

Grave's dissertation in its published form is less than 30 pages in length and includes 14 figures and 3 plates (Figure 7). The text is subdivided into parts based on bivalve anatomy. There is a brief introduction and also a brief 10-part summary at the conclusion of the text.

As neither of the authors is schooled in bivalve anatomy, we inquired of Brian Morton, Professor emeritus of Marine Ecology of The University of Hong Kong. Professor Morton is officially retired, but continues research in ecology and conservation and now lives in the United Kingdom. He built a prominent career in marine biology in Asia and is widely known for his efforts in marine conservation. Professor Morton is also acknowledged for his pioneering and ongoing work in bivalve anatomy. Professor Morton kindly read the published version of Grave's dissertation and offers the following comments:³⁰

“For its time, it is a remarkable piece of work in terms of the detailed understanding of the species' anatomy but also with regard to its skillful interpretation in the accompanying illustrations, which, in the absence of any evidence to the contrary, I assume Grave undertook.

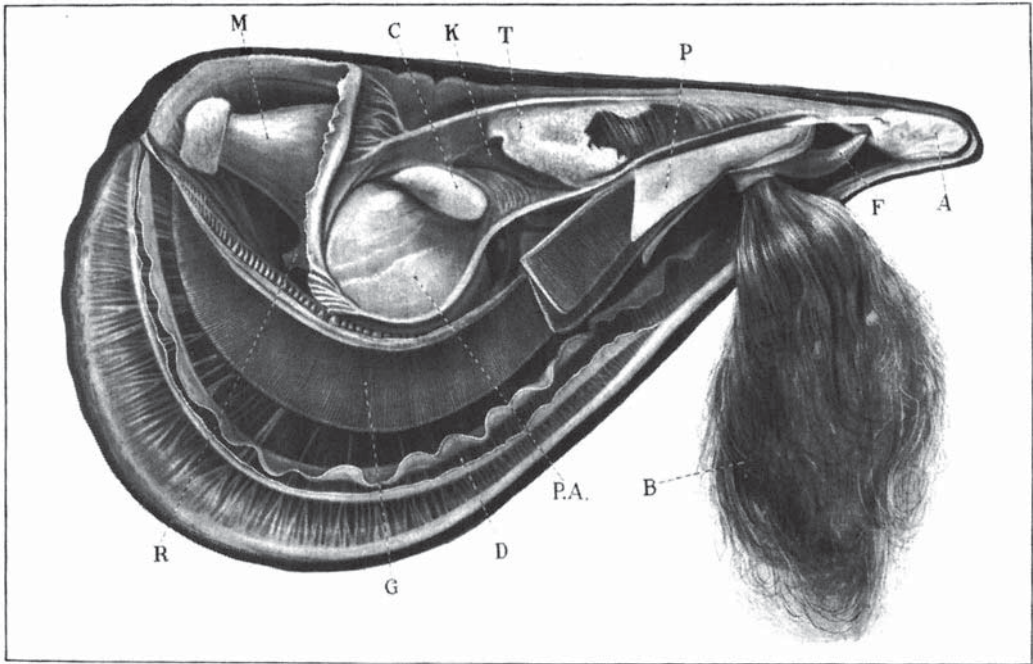


Figure 7. *Atrina rigida* (from B.H. Grave 1911, Bulletin of the Bureau of Fisheries 29: 409-439, plate XLVIII fig. 16.)

In fact, there are few people alive today who would match the quality of such anatomical drawings.”

“All in all, I would say that Grave was way ahead of his contemporaries in terms not only of his understanding of bivalve anatomy, but also the quality of the anatomical illustrations created and his interpretations of them”.

Finally, Professor Morton led us to a landmark paper by C.M. Yonge on a species in the related genus *Pinna*. In this work, C. M. Yonge credits Grave for important initial observations on anatomy in species of the family Pinnidae and is able to confirm some of Grave’s findings.³¹ First and most significant is Grave’s observation that the mantle lobes are free from the shell and that this feature makes repair of damage to the shell possible. As the shells of these bivalves are easily damaged, this adaptation to facilitate repair has major consequences for the ecology of individuals and health of populations. Second, the large portion of the shell that is exposed to seawater is made of the outer prismatic layer that is secreted by the outer lobe of the mantle and not the inner nacreous layer. Third, Yonge reports the organs in the visceral mass in *P. carnea* are similar to those found by Grave in *A. rigida*. Fourth, Yonge found in the case of *P. carnea* that individuals who come loose from the sediment are unable to re-establish themselves. Grave observed a similar inability in *A. rigida* unless specimens became partially re-embedded anterior end downward in the sediment.

4. Teaching Career

Benjamin Grave was a dedicated educator who, over the course of his career, taught undergraduates at six colleges and universities and the Marine Biological Laboratory, Woods Hole, Massachusetts. In chronological order, he was on the faculty of: Carleton College (1904-1906), Earlham College (1908-1909), the University of Wyoming (1910-1913), Knox College (1913-1920), Wabash College (1920-28), and DePauw University (1928-42). Few details have been preserved, but it is clear that he had experience with a wide range of biological topics, in the field and the laboratory.

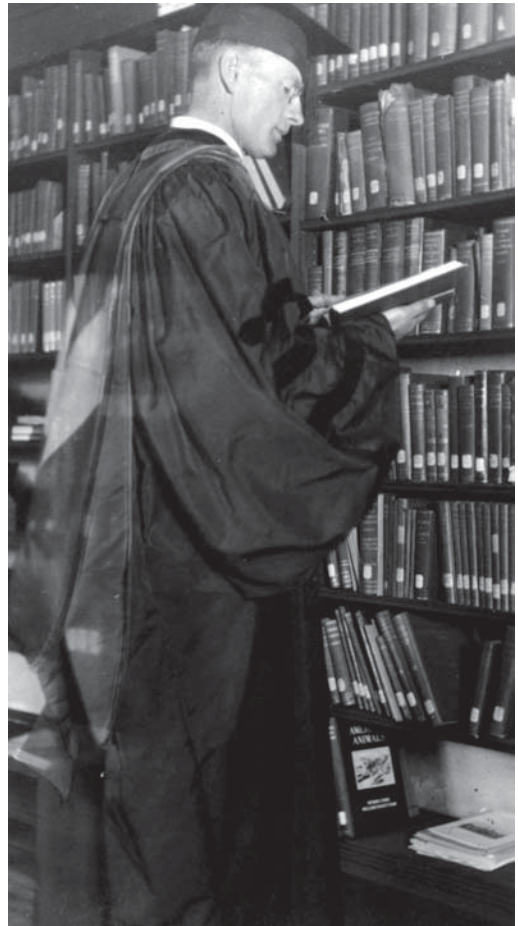
His earliest known teaching appointment was at Carleton College in Northfield, Minnesota, as Instructor in Biology. In the two years he spent there, he taught Invertebrate Zoology, Botany, and Plant Physiology and Anatomy. Professor Franz Exner praised his work in Biology and added that Grave also assisted the laboratory sections of Elementary Chemistry. Both Exner and his colleague Professor Lucian W. Chaney wrote glowing recommendations to Johns Hopkins University president Ira Remsen.³² Grave was well-liked and respected at Carleton, and they would have preferred to retain him, but they endorsed his returning to complete his doctoral studies.

Grave left Johns Hopkins for a second time for the 1908-09 academic year, returning to Earlham College. When Professor David W. Dennis, the head of the biology department, went on leave suddenly, Grave left Baltimore for Richmond, Indiana, to teach Comparative Anatomy and Plant Evolution and manage the laboratories. In the 1909 yearbook, *The Sargasso*, the students praised alumnus and now Assistant Professor Grave. They good-naturedly recalled his frugality and his chapel address opposing “Wishy Washy Sentimentalism.”³³ It is likely that Dennis had recommended the choice of Grave for that year. In 1906, he had written “I have known him and his family for a long time and would underwrite for Ben whatever he desires. He would not want what he could not do.”³⁴

Following graduation from Johns Hopkins University, Grave taught biology at the University of Wyoming, Laramie, Wyoming, from 1910-1913. Laramie was an isolated community in the early twentieth century, 80 km from the state capital of Cheyenne, over 1700 km from Grave’s family and friends in Indiana, and over 2700 km from Baltimore and the Atlantic coast. No detailed records of Grave’s teaching were preserved, but a few fragments document his time there. In October 1912, professor of botany Aven Nelson wrote that Professor Grave would produce an article on leaf miners,³⁵ but this entomological paper was never published. A cicada collected by Grave in Laramie is mentioned in the type description of *Okanagana gibbera* in 1927.³⁶ The only works that Grave produced while at Wyoming were on the avifauna of Wyoming, in collaboration with Ernest P. Walker.³⁷ The 1913 yearbook, *The Wyo*, includes Benjamin H. Grave, Ph.D, Professor of Zoology, and Ernest P. Walker is recorded as a member of the sophomore class.³⁸ Both Grave and Walker left Wyoming after the spring semester of 1913: Grave to do summer research at the Marine Biological Laboratory at Woods Hole, Massachusetts, and Walker to take a position as warden and inspector for the U.S. Bureau of Fisheries in Alaska.

Figure 8. B.H. Grave in the Science Math Center Library, Knox College (Courtesy of Knox College Archives)

Grave was appointed Professor of Biology at Knox College, Galesburg, Illinois, in 1913 replacing Professor Herbert V. Neal.³⁹ Knox College, a liberal arts college in the midwestern region of the United States, seemed a more congenial environment for Grave. Founded by a group of missionaries led by the Reverend George Washington Gale, it has been known for the moral character of its students and faculty. In October 1858, future president Abraham Lincoln debated Stephen A. Douglas on the Knox College campus. In the spring of 1914, the students described Grave thus: “Although a newcomer, Dr. Grave is no longer a stranger. He has gained the friendship and esteem of the college as a whole thru his versatile knowledge of human nature and his thoroughness in his courses.” The student authors also observed that “that laugh of Professor Grave’s: it’s the best one in school.”⁴⁰ Only one year after arriving at Knox, Grave published his



Laboratory Guide for a Course in Invertebrate Zoology (Appendix 1), almost certainly to fulfill the needs of his own classroom. In addition to teaching, Grave was also responsible for curating the Albert Hurd Museum.⁴¹ A natural history museum with over 20,000 specimens in the early twentieth century, the Hurd is now a teaching collection of approximately 1300 vertebrate specimens.⁴² A notable milestone during Grave’s tenure at Knox was his marriage to Earlham College alumna Lucile H. Moore (Figure 9), known as Lucy, on 14 September 1915. In 1920, Ben and Lucy Grave left Knox College to return home to Indiana.

Grave served on the faculty at Wabash College, Crawfordsville, Indiana, from 1920-1928.⁴³ Wabash College is an independent liberal arts college for men, founded by Presbyterians. Grave had a productive tenure at Wabash, with a devoted following of students. He was an energetic and athletic presence on campus who always walked or bicycled between his home and campus.⁴⁴ He took students with him to the Marine Biological Laboratory, Woods Hole, Massachusetts, for many summers (Figure 11),



Figure 9 (left). Lucile Moore Grave (Courtesy of Earlham College Archives)

Figure 10 (right). Ben Grave (Courtesy of Earlham College Archives)

including Joseph F. Oliphant (1906-1986).⁴⁵ Another distinguished student of Grave's was Willis H. Johnson (1902-1994), who went on to earn a Ph.D. at the University of Chicago and became the Head of the Biological Sciences Department at Wabash. Grave's faculty colleague Fergus Ormes recalled Grave as a somewhat controversial figure. Although the better students were devoted to him, the poor to average students found him "tough and unreasonable." He had a tendency to be perfectionistic, and was a formidable opponent when conflicts arose at faculty meetings. According to Ormes, Grave was adept both at laboratory work and in taking students out into the field, with memorable dinners around the campfire. Another of Grave's responsibilities at Wabash was curating the

Hovey Museum, the college's natural history museum, which had been established by botanist John Merle Coulter when he was on the faculty there.⁴⁶ Grave took a leave of absence in 1926-1927 to conduct research at Yale University as a Seessel Fellow. The following year was his last at Wabash, as he accepted an offer to head the Zoology Department at nearby DePauw University.

Grave spent the remainder of his professional career on the faculty of DePauw University in Greencastle, Indiana, approximately 50 km to the south of Crawfordsville, and only 35 km from his hometown of Monrovia. DePauw University, a coeducational liberal arts institution affiliated with the United Methodist Church, grew rapidly during the 1920s under President Lemuel H. Murlin. Grave was hired to bolster DePauw's teaching faculty, in order to serve a larger student population.⁴⁷ He was the head of the Zoology Department from 1928-1940, and continued to teach until 1942, when he transitioned to emeritus status due to health issues. Grave led the Zoology Department through its evolution in the 1930s - its move out of Middle College and into temporary quarters in the Science Annex, a frame building nicknamed "Termite Hall,"⁴⁸ and then into Harrison Hall in September 1940, newly opened and built on the site of Middle College, providing expanded space for the Zoology, Botany, Geology and Psychology departments.⁴⁹ Few details of his teaching at DePauw were preserved, but a 1933 article in the campus newspaper, *The DePauw*, gives a vivid glimpse. The Monday December 13th article related that Grave, having suffered a stroke the previous Friday, was at Indianapolis Methodist Hospital, where he was "directing his classes from the bedside."⁵⁰ A remarkable number of his students who majored in zoology, approximately 85 percent, went on to advanced study in zoology, medicine, or related subjects.⁵¹ The class of 1941 described an active "Dr. Grave" as a naturalist who loved to "roam in the woods" and remarked on his many years of summer research at the Marine Biological Laboratory at Woods Hole.⁵²

Grave took groups of as many as six students from DePauw to Woods Hole each summer in the 1930s, typically for the invertebrate zoology and embryology courses.⁵³ Zoology student Jay Smith spoke at the Evening Lectures at Woods Hole with Grave in 1935 on "Sex Inversion in *Teredo [navalis]* and its Relation to Sex Ratios".⁵⁴ Smith and Grave coauthored an article on that topic which was published in 1936 (Appendix 1). DePauw University did not have a natural history museum, but Grave continued collecting nevertheless. In 1931, he donated 5 specimens of salamanders, collected in Putnam County, Indiana, to the Field Museum in Chicago.⁵⁵

Grave taught embryology at the Marine Biological Laboratory from 1919-1936, a period spanning his tenure at Knox, Wabash, and DePauw. As mentioned above, he brought many of his undergraduate zoology students to Woods Hole with him for the summer, a great opportunity for undergraduates from the Midwest.⁵⁶ Grave and his students thrived in association with other students and faculty from around the United States, including Grave's older brother Caswell, who was also an instructor and investigator there. Three students' work was of a caliber that led to collaboration on publications: Ralph C. Downing (Wabash), Joseph F. Oliphant (Wabash), and Jay Smith (DePauw). It is thus not surprising that Professor and Mrs Grave designated part of their estate as a



Figure 11. B.H. Grave at Woods Hole, Massachusetts, 1921 (Courtesy of Marine Biological Laboratory Archives, <http://hpsrepository.mbl.edu/handle/10776/2433>)

scholarship fund for students at Knox, Wabash, and DePauw to study marine biology, with preference given for those attending the Marine Biological Laboratory.⁵⁷

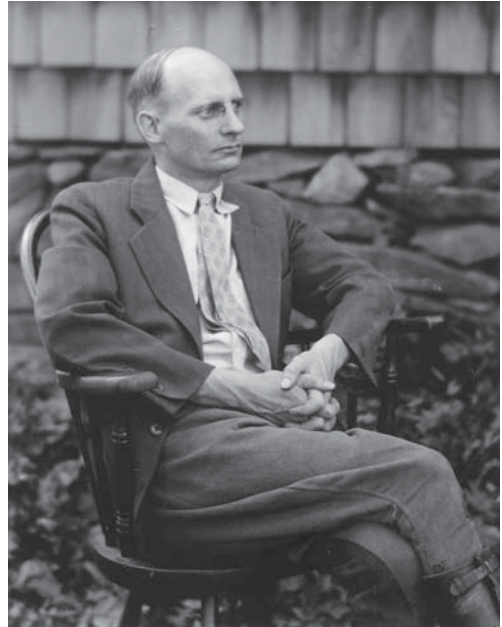
Throughout his career, Grave was active in professional associations. He was a member of the American Society of Zoologists, the Indiana Academy of Science, where he served as chair of the Zoology Section, and the American Association for the Advancement of Science, becoming a Fellow of the AAAS in 1915.⁵⁸ At Wabash College, he chaired the committee for relations with the National Education Association, a labor organization for teachers and professors in the United States.⁵⁹

5. Research and the Marine Biological Laboratory

We have already considered Grave's dissertation research on anatomy of the marine bivalve mollusk *Atrina rigida*, a species of commercial importance at the time of his investigations. Though his study reports in considerable detail about the species, for whatever reason, it has not been often cited in subsequent years. Leading specialists in bivalve anatomy and functional morphology, however, hold the work in high regard.

For the invertebrate biologist, likely the most surprising works in Grave's oeuvre are his collaborative study with Ernest Pillsbury Walker⁶⁰ (Figure 12) on the effects of land use change on avian species richness in Wyoming⁶¹ and his related single-authored publication regarding the influence of agricultural development on bird fauna⁶² that summarizes major ideas underpinning this survey. The Grave and Walker paper includes a discussion of how the conversion of prairie to agricultural land and the increasing human population associated with the establishment of farming affected species composition and

*Figure 12. Ernest Pillsbury Walker
(Smithsonian Institution Archives.
Image 94-515)*



richness of bird species. The survey also contains a list of all known species of birds to be found in Wyoming, new records for the state, and new breeding records. The study was conducted under auspices of the Department of Zoology at the University of Wyoming. Walker spent two summers in the field making personal observations. Data were acquired from previous collectors, most importantly W. C. Knight's study published in 1902.⁶³ Inquiries were made of residents about their observations and impressions of species identities and abundances before and after the introduction of significant agricultural development. Results indicated that certain species increased in number (Robin, Meadow Lark, Crow, Dove, Brewer's Blackbird and Cowbird). Some species described as rare by W. C. Knight were considered common by 1913. Finally, 45 species were found new to the state since the 1902 survey. Grave and Walker attributed the increase in number of species to agricultural growing of grain that provided seeds as food, tree plantings associated with towns and farm buildings creating new habitat that is rare, or mostly absent, in the prairie ecosystem, and irrigation for growing of crops providing an increase in sources of water. On the converse side, the authors report a subjective consensus among those interviewed that game birds were less abundant, presumably attributable to greater hunting pressure brought on by the increase in human population associated with agriculture. Grave and Walker emphasize the positive role of birds as predators on insects, many species of which are harmful to agriculture. Additionally, seed-eating birds were noted to have a beneficial effect in reducing weed populations and, concomitantly, a deleterious one in consumption of agriculturally important seed.

Grave and Walker conclude with several basic recommendations. First, they considered existing state laws concerning protection of species sufficient in coverage and that little could be gained by adding further legislation. Compliance with these regulations, however, they point out is critical to achieving the intended goals of any laws. Finally, the authors suggest that attracting birds to home settings would be fostered by planting trees for shelter, providing ample water and food, and by not maintaining cats as pets. Clearly, the vision of Grave and Walker that more species of birds present regardless of their origin is desirable stands at odds with today's conservation efforts to limit habitat destruction and introduction of alien species brought about through land use changes and their consequent effects.

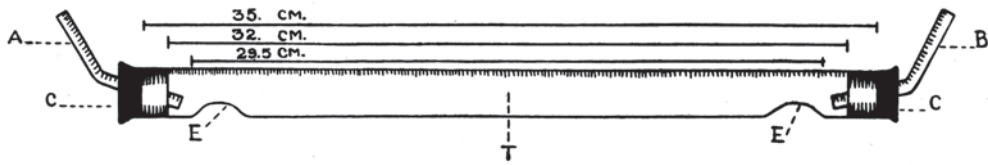


Fig. 1 *E*, elevation in floor of tube; *T*, experimental tube, 2 cm. in diameter and 29½ cm. long; *A*, feed tube through which sperm were introduced; *B*, feed tube through which eggs were introduced; *C*, cork stoppers.

Figure 13. Sperm tube apparatus (from B.H. Grave and R.C. Downing, 1928. *Journal of Experimental Zoology* 51(3), 384)

The major body of Grave's scholarly output focused on diverse aspects of the biology of marine invertebrates, particularly from the region of Woods Hole, Massachusetts. These studies range over 20 species in 7 phyla (Appendix 2). Such taxonomic breadth is a credit to Grave's broad interests and apparent fascination with natural history. Not only was Grave able to successfully conduct research using diverse fauna, he also investigated a broad array of problems in life history biology, including: anatomy, life cycles, spawning, egg longevity and fertilization capability, sperm longevity and fertilization capability, protandric hermaphroditism, and culture techniques.

Grave enjoyed "tinkering" and creating novel apparatuses and clever experimental designs to test some of his ideas. Most interesting is the device designed to test sperm swimming speed and swimming distance (Figure 13). Grave and his student Ralph C. Downing⁶⁴ set out to improve on the experimental design created earlier by the Scottish naturalist James Fairlie Gemmill to test gamete viability.⁶⁵ Gemmill was concerned about the accuracy of sperm locomotion measurements using dishes with a large air-water surface area because of factors such as air currents on the water surface creating mixing that would result in passive dispersal of sperm rather than translocation by active swimming. In an attempt to avoid this pitfall, Gemmill employed narrow cross-section tubes of varying lengths as a more accurate way of determining sperm swimming speed. Unfortunately, the narrow diameter tubes accentuated boundary effects on sperm movement thus making Gemmill cautious of these data as well. Grave and Downing's apparatus was designed to overcome or at least minimize these limitations. The design was based around a tube-like chamber and introducing unfertilized eggs at one end of the chamber and sperm at the opposite end. Hillocks were placed near the end of tubes but distal to where gametes were introduced, creating shallow wells in order to reduce passive dispersal of gametes. Gametes were introduced into the wells. Time from introduction of sperm to observable fertilization of eggs at the opposite end of the tube, as evidenced by a cortical reaction having taken place in the eggs, was then measured and converted to swimming speed. Grave and Downing attempted to avoid wall effects by increasing the diameter of the chamber over the sizes used by Gemmill. By the use of carmine particles, the authors tested for currents that might result in passive transport of gametes. They found that eggs

sank to the bottom and did not cross the hillock and they reported no evidence of sperm passively diffusing across the hillock at the other end of the chamber. In 1934 Grave modified the design even further and devised a way to submerge the tube to eliminate any effects of air currents on water mixing within the tube.⁶⁶ Considering that Grave had no special understanding of fluid dynamics, he did an admirable job of thinking through potential problems in design.

Grave published two journal articles on bryozoans⁶⁷ and one chapter in a multi-authored volume on culture methods.⁶⁸ These studies focused primarily on *Bugula simplex* (as *B. flabellata*).⁶⁹ Included in the paper are some data on *B. turrita* also from the Woods Hole region.

The most cited of all Grave's output is his 1930 paper in *Biological Bulletin* on the natural history of *B. simplex* (as *B. flabellata*) with comments on *B. turrita*.⁷⁰ This broad-based descriptive account includes information on reproductive season, larval release and behavior, settlement and metamorphosis. Grave carefully notes comparisons of his findings with those of previous workers, primarily in France and Germany. Again, Grave reveals his fascination with experimental design. By manipulation of the light regime, Grave documents that release of larvae from parental colonies is a light-triggered event. He examined phototactic responses at different stages of larval life by shifting the source of light using a mirror, and documented that larvae settle away from the direction of incident illumination. In important ways, this paper set the stage for a large body of subsequent work that remains ongoing a century later. But Grave's study is not without some oversights. For example, in his analysis of morphogenetic movements in the rearrangement of tissues during metamorphosis, Grave does not mention the involution of the corona and uplift of the walls of the metasomal (internal) sac in establishment of the lateral aspects of the ancestral body wall. Though a critical step in metamorphosis, it would have been a difficult one to observe in conventional light microscopy of the day.

One fascinating aspect of Grave's 1930 study has been overlooked by subsequent investigators. Grave reported that *Bugula turrita* occurs in Vineyard Sound, but not Eel Pond and *B. simplex* [as *B. flabellata*] was found in Eel Pond, but not Vineyard Sound. Yet the two bodies of water communicate freely. When Grave reciprocally transplanted colonies of these species, they did not survive and, instead, died within months to a year. Grave proposed that the inability to survive might have been attributable to different properties of water flow between Vineyard Sound and Eel Pond, with the latter being more sheltered. Grave pointed to similar differences in occurrence of species of hydroids between the two localities. In their manual on culture methods,⁷¹ Costello and Henley reported in 1971 the same distributions of *B. simplex* (as *B. flabellata*) and *B. turrita*. When *B. turrita* became successfully established in Eel Pond is undocumented. This species remains at the present time a conspicuous member of the Eel Pond fouling community.

Thus we come full circle in one arena of Grave's research agenda: from non-native birds entering Wyoming due to conversion of prairie to agricultural use to his failed transplantation attempts involving species of *Bugula* in the Woods Hole region. Although his point of view is quite different from the modern conservationists, he provides some

good historical data and insights on the contemporary thought of his day.

Osburn⁷² stated explicitly in his 1910 monograph on bryozoans of the Woods Hole region that a third congener, *B. stolonifera* (as *B. avicularia*)⁷³ was not present in any collection from the Woods Hole area. Rogick, however, while not including *B. stolonifera* (as *B. avicularia*) in her 1964 key to bryozoans of Woods Hole,⁷⁴ does provide a figure of this species. She may have chosen this action because *B. stolonifera* might have been present, but was sufficiently rare in occurrence to not merit inclusion in the key. Gooch and Schopf (1970)⁷⁵ employed specimens of *Schizoporella errata* from Eel Pond and Green Pond along with *B. stolonifera* collected in Eel Pond for their pioneering study of population genetics of marine bryozoans. They do not mention, however, the history of *B. stolonifera* in the context of *B. avicularia* in Eel Pond. Karl Kaufmann's 1971 study of *avicularia* was based on *B. simplex* and *B. stolonifera* from Eel Pond.⁷⁶ Again, no mention of the history of *B. stolonifera* was included. Finally, *B. stolonifera*, *B. simplex* and *B. turrita* were reported to co-exist in Eel Pond by 1982.⁷⁷ The arborescent cheilostome fauna occurring in Eel Pond continues undergoing change to the present day.⁷⁸

The 1933 article by Grave⁷⁹ on life history parameters of some Eel Pond invertebrates covers a 10-year survey of rates of growth, time of sexual maturity, and duration of life. This study focuses on *Obelia commissuralis*, *Balanus eberneus*, *Hydroides hexagonus*, and *Botryllus gouldii*. Only brief mention is made of *Bugula simplex* (as *B. flabellata*). Grave amends several quite minor points mentioned in his major 1930 paper. These changes include the observation that the first avicularium develops in colonies of four autozooids rather than later as noted in 1930; at the eight autozoid stage avicularia are present on the second, third, and fourth autozooids; and the everted metasomal (= internal) sac becomes branching and stolon-like in form rather than disc-like as stated in 1930. Comment on this article is included here only for purposes of thoroughness of coverage of Grave's observations on bryozoans.

Finally, Grave contributed a chapter on culture methods for *Bugula simplex* (as *B. flabellata*) and *B. turrita* to a multi-authored volume on culture techniques of invertebrates.⁸⁰ This chapter and five additional ones Grave authored on different species of invertebrates are products of his many years of engagement with the natural history of marine invertebrates at Woods Hole. Most of these likely derive in large measure from his extensive teaching experience at the Marine Biological Laboratory mentioned in previously in Section 4.

6. Personal Life and Later Years

Grave had an active personal life, enjoying outdoor activities and cultural events. Until his health declined, he was known for taking long walks, especially "moonlight walks" with his wife. While at Wabash College, Ben and Lucy socialized with other faculty couples, reading plays aloud at each other's homes.⁸¹ They both enjoyed listening to music, especially Beethoven. Cleveland P. Hickman, a zoology colleague from DePauw University, wrote: "By nature he was sympathetic and generous and every worthy cause

received willing support in his hands. Nothing afforded him greater enjoyment than the study of nature in all of its aspects and he developed an aesthetic appreciation of outdoor beauty”.⁸² His colleague Will E. Edington remembered Grave as “deeply interested in spiritual values and the problems of human welfare and ... a bitter foe of intolerance or tyranny in any form either on or off the campus.”⁸³

Grave’s unpublished work *The Destiny of Man* (Appendix 1) consists of a set of five essays that are works of encouragement, with themes of progress, spirituality, and optimism. They appear to be addresses to undergraduates and may well have been notes from which he spoke: typewritten pages with hand-drawn illustrations, as well as corrections and additions in handwriting. Grave introduces three scholarly figures with differing points of view: Jacques Loeb (1859-1924) with a mechanistic view of science and the world, Herbert Spencer Jennings (1868-1947) emphasizing experimentation and experience, and Quaker theologian and educator Rufus Jones (1863-1948) on mysticism and spirituality. When discussing Loeb and tropism, Grave includes examples of the behavior of *Bugula* larvae. Throughout, Grave expresses his own deeply ingrained faith and his appreciation of beauty in nature. Because of references to popular American sports figure Red Grange, and the statesmen Aristide Briand and Gustave Stresemann (Nobel Peace Prize laureates in 1926), it was likely written in the mid-1920s for the Wabash College students.

Although Quakers have historically been pacifists, some, including members of the Grave family, have served in the military, especially when issues of justice were at stake. Ben’s father, Thomas Clarkson Grave, served in the Union Army, Indiana 33rd Infantry Regiment, during the United States Civil War.⁸⁴ Ben’s younger brother Floyd commanded a medical laboratory in France attached to the 90th division of the American Expeditionary Forces in World War I.⁸⁵ Caswell and Caswell’s son Thomas also served in World War I with the Chemical Warfare Service in Washington, DC.⁸⁶ Ben and his younger brother Thomas registered for both World War I and World War II, as was required, but were not drafted for service. Ben’s draft registration cards reveal his physical description, not available from other sources. In 1918, the registration card reflected a man in his prime: a professor at Knox College, Galesburg, Illinois, height of 5’ 11” (180cm) and weight of 160 lbs (72 kg), with blue eyes and brown hair. Twenty four years later, in 1942, he was retired in Greencastle, Indiana, still at the same height but only 127 lbs (58 kg).⁸⁷

Although the distinctive traditional dress and speech of the Quakers diminished in use in the nineteenth and early twentieth centuries,⁸⁸ a remnant of the tradition is found in letters among the Grave and Moore families. While they used standard American grammar in business communications, Ben and Lucy used the traditional “thee” and “thy” forms when writing to family members. Ben’s letter to Lucy in December 1924 contains this usage and reveals much of his life at that time: he expresses his devotion to Lucy, shares remembrances of his father who had passed away earlier that year, and also discusses plans for his research on invertebrates. Letters from Lucy underscore what others observed of her: a great appreciation of beauty, a quick wit, absolute devotion to her husband, and a warm and diplomatic manner.⁸⁹



Figure 14. Caswell Grave (Courtesy of the Marine Biological Laboratory Archives, <http://hpsrepository.mbl.edu/handle/10776/2868>).



Figure 15. B.H. Grave ca. 1935 (Courtesy of DePauw University Archives and Special Collections)

Family relationships were important to both Ben and Lucy Grave. Both were from close-knit, devout Quaker families who vigorously encouraged education. With the exception of three years in Wyoming, Ben lived with or near relatives for the rest of his life. In addition to their association with Earlham College noted above, all four of the Grave brothers attended Johns Hopkins University,⁹⁰ first Caswell (Figure 14) and then various combinations of the brothers, depending on the year, living with Caswell and his wife Josephine (d. 1951) in Baltimore while Caswell was on the faculty there.⁹¹ After his marriage to Lucy Moore in 1915, Grave maintained ties with both his own family and the Moores. Because they were both Earlham alumni, Ben and Lucy's holiday visits to Mrs. Moore, Ben's visiting lectures, etc., were chronicled in the Earlham campus newspaper.⁹² Every summer from 1919-1936, Ben and his brother Caswell were both in residence at Woods Hole with their families.⁹³ Caswell's son Thomas Brooks Grave, was also a fixture at Woods Hole, serving as the "Person in Charge" of the Chemical Room at the Marine Biological Laboratory from 1920-25.⁹⁴ Lucy maintained close ties with her mother, Mary Thorne Moore (1847-1925) and siblings, Anna M. Cadbury (1873-1932), Grace E. Moore (1876-1953), and Willard E. Moore (b. 1884). Her sister Grace remained at the home

where they had grown up, on the Earlham Campus, where Lucy would join her after Ben's death in 1949. The Moore family home at 430 College Avenue, which they called Twin Willows, is now the Marketing and Communications Office at Earlham College.

Grave's health declined in the 1930s. He suffered a stroke in 1933⁹⁵ and a severe case of shingles in 1936.⁹⁶ He retired for health reasons in 1942, and was cared for by Lucy at their home in Greencastle, Indiana, until his last days. Colleagues from Wabash and DePauw visited him at home after his retirement, and remarked on Lucy's dedication.⁹⁷

Benjamin Grave passed away on Monday, 24 January 1949, at Central Hospital, Indianapolis, Indiana, from complications following a fall and broken hip.⁹⁸ Faculty colleagues joined with friends and neighbors at a Quaker style memorial service held at the Graves' home on Friday, 28 January. Clyde E. Wildman (1889-1955), then President of DePauw University and an ordained Methodist minister, led the service.⁹⁹ Grave was remembered as a beloved colleague and mentor, his life and career characterized by "simplicity, sterling integrity and fearless defense of what he believed to be right and true."¹⁰⁰ He is buried in Earlham Cemetery, Richmond, Indiana, next to his wife (Figure 16) and in close proximity to Joseph and Mary Thorne Moore.¹⁰¹



Figure 16. Gravestone of B.H. Grave, Earlham Cemetery, Richmond, Indiana, 29 May 2013
(Courtesy of Friends Collection, Earlham College)

7. Acknowledgements

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Notes

- 1 Dates for Thomas Clarkson Grave and Elizabeth Hubbard Grave from gravestones in West Union Cemetery, Monrovia, Indiana.
- 2 *Biographical and Genealogical History of the State of Delaware*, vol. 1, J.M. Runk, Chambersburg, PA, 1899, 473.
- 3 Hubbard family information confirmed in: United States of America, Bureau of the Census. *Seventh Census of the United States, 1850*. Census Place: Monroe, Morgan, Indiana. Micropublication roll M432_162, page 129A, image 264.
- 4 *Thomas Graves, Quaker of Newcastle Co., Delaware and His Descendants*, <http://www.gravesfa.org/gen085.htm>, accessed 3 October 2013.
- 5 P. Montgomery, *Indiana Coverlet Weavers and their Coverlets*, Hoosier Heritage Press, Indianapolis, 1974, 56.
- 6 D.I. Grave, "Coverlet", 1838, Art Institute of Chicago catalog, <http://www.artic.edu/aic/collections/artwork/72456>, accessed 3 October 2013.
- 7 The Society of Friends is organized into groups called "meetings". The term meeting is used for congregational units as well as larger groups. A yearly meeting is a larger group of people than a monthly meeting, for example, and would be composed of several monthly meetings. These meetings maintained strict codes of conduct in the 19th century, including dress and speech and prohibiting activities such as dancing or drinking alcohol. David Isaac Grave was cited by Whitewater Monthly meeting for being lax in disciplining his children amongst other

offenses.

- 8 T.C. Grave family information confirmed in: United States of America, Bureau of the Census, *Tenth Census of the United States, 1880*, Census Place: Monroe, Morgan, Indiana, Enumeration District: 263. Micropublication roll 301, Film 1254301, page 41B, image 0086.
- 9 F.A. Battey and F.W. Teeple, *Counties of Morgan, Monroe and Brown, Indiana: Historical and Biographical*, F.A. Battey & Co., Chicago (1884)126-129; Current information for West Union Friends Meeting at <http://www.fwccamericas.org/MeetingSearch.aspx?n=West+Union+Friends+Meeting>; Friends United Meeting information <http://fum.org/>.
- 10 W. Norman Brown, *Johns Hopkins Half-Century Directory: A Catalogue of the Trustees, Faculty, Holders of Honorary Degrees, and Students, Graduates and Non-graduates 1876-1926*, Johns Hopkins University, Baltimore (1926) 137.
- 11 Anne Thomason, Earlham College Archives, personal communication, 20 August 2013.
- 12 David Worth Dennis (1849-1916) was a member of the science faculty at Earlham College from 1884 to 1916, and a friend and mentor to Benjamin Grave. He received his A.B. degree at Earlham College in 1873 and his Ph.D. in Geology from Syracuse University in 1899 (*Alumni Record and General Catalog of Syracuse University*, F. Smalley (ed.), Syracuse, N.Y. (1889) 599, 653). In the course of his career, D.W. Dennis taught chemistry, biology and geology at Earlham College, serving as the head of the Biology Department for many years. ('David W. Dennis, A.B., A.M., Ph.D.' *Biographical and Genealogical History of Wayne, Fayette, Union and Franklin Counties, Indiana*, Lewis, Chicago (1899) 17-19.) He was also an Orthodox Quaker minister.

His son, William Cullen Dennis (1878-1962) was the president of Earlham College from 1929 to 1946. (Dennis Family Papers, 1867-1988, Friends Collection, Earlham College Archives, <https://archives.earlham.edu/?p=collections/findingaid&id=49>, accessed 17 October 2013.) The younger Dennis was a close friend of Ben and Lucy Grave, and Lucy's sister Grace (letter from W.C. Davis to B.H. Grave, 21 December 1936, Earlham College Archives).

- 13 Joseph Moore (1832-1905) was a major figure in science and education in 19th century Indiana. He studied at Friends Boarding School (which would become Earlham College in 1859), Richmond, Indiana, then began teaching there in 1853. Moore was a student at Harvard University from 1859-1861, receiving the S.B. degree from Harvard's Lawrence Scientific School in 1861. At Harvard, he was a student of Louis Agassiz, Asa Gray, and Jeffries Wyman, and was influenced by each. He developed a neo-Lamarckian theory of evolution which was consistent with his Quaker beliefs, and is believed to be the first educator to teach about evolution in Indiana. (W. Cooper, 'Joseph Moore: Quaker Evolutionist', *Indiana Magazine of History* 72 (2) (1976) 123-137.)

Moore returned to Indiana in 1861 to serve on the faculty of Earlham College. He was president of Earlham College from 1868-1883, then in 1883 moved to North Carolina where he taught and served as principal at New Garden Boarding School, which is now Guilford College. He returned to Earlham in 1888 to teach botany and geology. He started the natural history museum at Earlham College as a teaching collection in 1853, and continued to collect specimens and develop the museum over the next several decades. ('Joseph Moore, M.A.' *Biographical and Genealogical History of Wayne, Fayette, Union and Franklin Counties, Indiana*, vol. 1, Lewis, Chicago (1899)190-192.) It was re-named the Joseph Moore Museum in 1905, and is currently a resource for the Earlham community and the general public.

In addition to his academic leadership, Moore was also a respected religious figure, recorded as a minister by the Society of Friends in 1865. Following the U.S. Civil War, he led efforts to assist Quakers in North Carolina. ('Joseph Moore' <http://www.earlham.edu/about/>

- campus-history/presidential-gallery/joseph-moore/, accessed 21 May 2013.)
- 14 "Benjamin H. Grave", *Wabash Bulletin* 19 (4) (1920) 8-9.
 - 15 Application for Admission, Johns Hopkins University, Benjamin Harrison Grave, 1 October 1903, section VI, student files, Johns Hopkins University Archives.
 - 16 'The Biological Laboratory 15th Season', *Sixteenth Yearbook of the Brooklyn Institute of Arts and Sciences* (1904) 198-202.
 - 17 Transcript for Benjamin Harrison Grave, University of Chicago, Summer 1905, Office of the University Registrar. Additional information supplied by Timika Hoffman-Zoller, Office of the Registrar, personal communication 22 July 2013.
 - 18 B.H. Grave to I. Remsen, 5 April 1906, student files, Johns Hopkins University Archives.
 - 19 *The Carletonian*, June 11, 1906 as communicated by Eric Hillemann, Carleton College Archivist, personal communication 13 September 2012.
 - 20 B.H. Grave to I. Remsen, note 18.
 - 21 'Win Relay by Foot: Georgetown Runners', *Washington Post*, 10 March (1907) S1. Grave finished second in the 440 yard open-handicap race, a track and field event held at Georgetown University on 9 March 1907. Johns Hopkins University won the Hickman and White Trophy for the institution with the greatest number of total points.
 - 22 B.H. Grave, 'Anatomy and physiology of the wing-shell *Atrina rigida*', *Bulletin of the Bureau of Fisheries* 29 (1911) 409-439, pls. XLVIII-L. [Published version]
 - 23 E.G. Conklin, 'William Keith Brooks 1848-1908', National Academy of Sciences, Washington, D. C. (1913) 88 pp.
 - 24 M. W. Fincham, 'The oyster dreams of W. K. Brooks: Could science save a seafood industry?' *Chesapeake Quarterly*, Maryland Sea Grant, April 2013, <http://ww2.mdsg.umd.edu/CQ/V12N1/main3/>, accessed 18 October 2013.
 - 25 W. K. Brooks, *The Oyster*, The Johns Hopkins Press, Baltimore, Maryland (1891) 230 pp.
 - 26 D. M. McCullough, 'W. K. Brooks's role in the history of American biology', *Journal of the History of Biology* 2 (2) (1969) 411-438.
 - 27 *American Men of Science*, 3rd edition, J. M. Cattell and D.R. Brimhall (eds.) Science Press, Garrison, NY (1921) 15.
 - 28 E.A. Andrews, 'Report upon the Annelida Polychaeta of Beaufort, North Carolina', *Proceedings of the U.S. National Museum* 14 (852) (1891) 277-302.
 - 29 *American Men of Science*, 3rd edition, J. M. Cattell and D.R. Brimhall, eds. Science Press, Garrison, NY (1921) 15.
 - 30 Personal communication from Brian Morton to Robert Woollacott dated 30 June 2013.
 - 31 C. M. Yonge, 'Form and habitat in *Pinna carnea* Gmelin', *Philosophical Transactions of the Royal Society* 237 (648) (1953) 335-374.
 - 32 L.W. Chaney to I. Remsen, 5 April 1906; F.F. Exner to I. Remsen, 4 April 1906, student files, Johns Hopkins University Archives.
 - 33 *The Earham Sargasso of 1909*, 2 (1909) 53, 58.
 - 34 D.W. Dennis to I. Remsen, 22 May 1906, student files, Johns Hopkins University Archives.
 - 35 A. Nelson, 1912, 'Horticultural Column', *Wyoming Farm Bulletin* 2 (4) (1912) p. 223.
 - 36 W.T. Davis, 'New cicadas from the western United States with notes on several other species', *Journal of the New York Entomological Society* 35 (1927) 373-386.
 - 37 Ernest Pillsbury Walker (1891-1969), subsequent to his study at the University of Wyoming, became the most prominent mammalogist of the twentieth century. His three-volume treatise *Mammals of the World* stands as a monument to his scholarship and devotion to mammals and their conservation. Walker was born in Missouri and completed his formal education at the

- University of Wyoming, never earning the Ph.D. He moved immediately after his stay at Wyoming to the Territory of Alaska where he worked for the U.S. Bureau of Fisheries. He later spent time in government service with the U.S. Biological Survey in California and Arizona and then returned to Alaska. In 1930, he was appointed assistant director of the Smithsonian Institution's National Zoological Park in Washington, D. C. where he would remain for the duration of his career. Walker officially retired in 1956, but stayed on at the zoo where he began the daunting process of assembling *Mammals of the World*, a massive work that was published in 1964. This treatise reported on 1044 known genera of recent mammals (R.H. Manville, 'Mammals in review', *Science* 146 (3649) (1964) 1285-1286).
- 38 *The Wyo*, 5 (1913) 17, 48.
- 39 'Among the Faculty', *American Educational Review* 34 (12) (1913) 621.
- 40 *1915 Gale: the Knox College Annual*, Galesburg, IL, 25 (1914) np.
- 41 'Educational Directory 1916-17', *U.S. Dept. of the Interior, Bureau of Education Bulletin* 43 (1917) 140.
- 42 F.J.H. Merrill, 'Natural History Museums of the United States and Canada', *Bulletin New York State Museum* 62 (1903) 41; James Mountjoy, Knox College, personal communication, 31 July 2013.
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- 44 Fergus Ormes was a colleague and neighbor of Grave's who was on the faculty at Wabash College from 1921-1958. He taught economics and was the College Comptroller from 1929-1958. His notes on Grave were written after he attended Grave's memorial service, and are part of a large collection of Ormes' observations of his contemporaries. F. Ormes, Personal Papers, 28 January 1949, Robert T. Ramsay, Jr. Archival Center at Wabash College.
- 45 After graduating from Wabash College, Joseph Oliphant (1906-1986) pursued graduate study at Johns Hopkins University. He earned the Ph.D. in Biology in 1935, with a dissertation 'The effect of chemicals and temperature on reversal in ciliary action in *Paramecium*', *Physiological Zoology* 11 (1) (1938) 19-30. He taught in the Department of Biological Sciences at Stanford University from 1938-1978.
- 46 The natural history collection at Wabash was based on donated specimens organized by Edmund O. Hovey (1801-1877), a founder of the college who taught geology and chemistry. Botany professor John Merle Coulter, who was at Wabash from 1879-1891, moved, organized and developed the collection, naming it in honor of Hovey in 1881. In Grave's era, the museum occupied four rooms in South Hall and the major categories collected were fossil vertebrates, crinoids, rocks and minerals, and Native American items. The museum collections were dispersed in 1950, with the fossils going to the Chicago Museum of Natural History (Field Museum) and botanical specimens to the Brooklyn Botanical Garden. (*Handbook of American Museums*, The American Association of Museums, Washington DC (1932) 152; Elizabeth Swift, Wabash Archives, personal communication, 27 August 2013; *Museum Work* 8 (5) (1926) 135.
- 47 C.J. Phillips et al., 'DePauw between the Wars' chap. 3 in S.Y. Loong (ed.), *DePauw University Pictorial History*, E-history edition, (2003) p.3 <http://my.depauw.edu/library/archives/ehistory/index.htm>, accessed 10 October 2013.
- 48 Cleveland P. Hickman, Jr., personal communication, 25 September 2013.
- 49 C.J. Phillips et al., note 47, p. 9.
- 50 'Prof. B.H. Grave Suddenly Stricken', *The DePauw* 33 (37) (1933) 1.
- 51 W. E. Edington, note 43.

- 52 *Mirage Yearbook*, DePauw University, Greencastle, Indiana (1941) 30.
- 53 C.P. Hickman, 'Benjamin Harrison Grave', *Anatomical Record* 106 (3) (1950) 438-439.
- 54 'The Marine Biological Laboratory thirty-eighth report for the year 1935...' *Biological Bulletin* 71 (1) (1936) 31.
- 55 *Field Museum News* 2 (1) (1931) 2. According to the specimen catalog of the Field Museum, the species donated were *Eurycea cirrigera*, *E. longicauda*, *Plethodon cinereus*, *P. dorsalis*, and *P. glutinosus*, all collected by Grave in Putnam County, Indiana, in 1930. <http://fieldmuseum.org/explore/department/zoology/amphibians-and-reptiles/collections>, accessed 9 July 2013.
- 56 'Annual Report of the Marine Biological Laboratory...' *Biological Bulletin (1920-1940)*. Each report includes names of students who attended MBL with Grave, identified by name and college. More information and class lists are available at <http://history.archives.mbl.edu/courses>.
- 57 Lucy Moore Grave Bequest, 2013-2014, *Wabash College Academic Bulletin*, (2013) 224.
- 58 W.E. Edington, note 43.
- 59 'B.H. Grave Heads Committee', *Wabash Bulletin* 25 (4) (1928) 1.
- 60 note 37.
- 61 B.H. Grave and E.P. Walker, 'Wyoming birds and their value to agriculture', *University of Wyoming Bulletin* 12(6) (1916a) 1-137; B.H. Grave and E.P. Walker, *The Birds of Wyoming with an explanation of recent changes in their distribution, economic aspects also considered*, University of Wyoming, Laramie, Wyoming, 1913 [1916b] 137 pp. [1913 is printed on the cover, but an author's note from 1916 states that printing was delayed and post-1913 data added. Grave preferred this title over the edition published as a *University of Wyoming Bulletin*.]
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- 63 W.C. Knight, *The Birds of Wyoming*, Wyoming Experiment Station, Laramie, Wyoming (1902).
- 64 B.H. Grave and R.C. Downing, 'The longevity and swimming ability of spermatozoa', *Journal of Experimental Zoology* 51 (3) (1928) 383-388.
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- 67 B.H. Grave, 'The natural history of *Bugula flabellata* at Woods Hole, Massachusetts, including the behaviour and attachment of the larva', *Journal of Morphology* 49 (2) 1930 355-384; B.H. Grave, 'Rate of growth, age at sexual maturity, and duration of life of certain sessile organisms, at Woods Hole, Massachusetts', *Biological Bulletin* 65 (3) (1933) 375-386. [Life history of *B. flabellata* on p. 384.]
- 68 B.H. Grave, '*Bugula flabellata* and *B. turrita*', in P.S. Galtsoff et al.(eds.), *Culture Methods for Invertebrate Animals*, Comstock, Ithaca, NY (1937) 178-179.
- 69 J.S. Ryland and P.J. Hayward, *Marine Flora and Fauna of the Northeastern United States. Erect Bryozoa*, NOAA Technical Report, NMF 99 (1977) 1-47.
- 70 B.H. Grave, 'The natural history of *Bugula flabellata* at Woods Hole, Massachusetts, including the behaviour and attachment of the larva', *Journal of Morphology* 49 (2) (1930) 355-384.
- 71 D.P. Costello and C. Henley, *Methods for Obtaining and Handling Marine Eggs and Embryos*, 2nd ed., Marine Biological Laboratory, Woods Hole, Massachusetts (1971) 247 pp.

- 72 R.C. Osburn, 'The Bryozoa of the Woods Hole region', *Bulletin of the Bureau of Fisheries* 30 (1912) 203-266.
- 73 It appears there is no single publication that explicitly deals with *Bugula avicularia* being incorrectly identified in material from Eel Pond and that the true identity of these specimens is *B. stolonifera*. Maturo (F.J.S. Maturo Jr., 'Bryozoa of the southeast coast of the United States: Bugulidae and Beaniidae (Cheilostomata: Anasca)' *Bulletin of Marine Science* 16(3) (1966) 556-583) states that *B. avicularia* reported to occur along the east coast of North America is likely *B. stolonifera*, but he makes no specific mention of material in Eel Pond. Maturo points out that Verrill, however, reported *B. avicularia* (USNM 4981) from "Ram Island Ledge" which Maturo suggests is Great Harbor, Woods Hole. Maturo, however, refers these specimens to *B. fulva*. That *B. avicularia* and *B. stolonifera* are, in fact, distinct species is made quite clear by Ryland (1960) – see Table 2, page 99 for comparisons of closely related species (J.S. Ryland, 'The British species of *Bugula* (Polyzoa)' *Proceedings of the Zoological Society of London* 134 (1960) 5-105.
- 74 M.D. Rogick, 'Phylum Ectoprocta', in R.I. Smith (ed.), *Keys to the Marine Invertebrates of the Woods Hole Region*, Contribution No. 11, Systematics-Ecology Program, Marine Biological Laboratory, Woods Hole, Massachusetts (1964) 165-187.
- 75 J.L. Gooch and T.J.M. Schopf, 'Population genetics of marine species of the phylum Ectoprocta', *Biological Bulletin* (2) (1970) 138-156.
- 76 K.W. Kaufmann, 'The form and function of the avicularia of *Bugula* (Phylum Ectoprocta)', *Postella* 151 (1971) 1-26.
- 77 M.S. Brancato and R. M. Woollacott (1982). The effect of microbial films on larval settlement in three species of *Bugula* (Bryozoa). *Marine Biology* 71(1) 51-56.
- 78 Since the establishment of *Bugula simplex*, *B. stolonifera*, and *B. turrita* in Eel Pond, a fourth, *B. neritina*, has appeared (C.H. Johnson, personal observation). This cosmopolitan species is a common component of fouling communities in tropical and subtropical waters worldwide. Though abundant and well-established south of Massachusetts, *B. neritina* has been sighted only occasionally in Massachusetts (J.E. Winston and P.J. Hayward, 'The Marine Bryozoans of the Northeast Coast of the United States: Maine to Virginia', Memoir 11, Virginia Museum of Natural History, Martinsville, VA. (2012) 180 pp.)

In an important study published in 2003 by McGovern and Hellberg (T. M. McGovern and M.E. Hellberg, 'Cryptic species, cryptic endosymbionts, and geographical variation in chemical defenses in the bryozoan *Bugula neritina*', *Molecular Ecology* 12 (5) (2003): 1207-1215) on cryptic species of *B. neritina*, the authors utilized material collected from Connecticut to Louisiana. The outgroups for their molecular analyses, *B. stolonifera* and *B. turrita* were collected from Woods Hole. Had *B. neritina* been obtainable at Woods Hole, the authors would have likely reported its presence and included genetic analysis of such specimens in their study as it would have extended the distribution range used in their investigation. Consequently, we place the time of introduction of *B. neritina* after 2003 and by August 2007, when it was first observed by C. H. Johnson (C. H. Johnson, personal observation). Since 2007, *B. neritina* has become a stable member of the Eel Pond fouling community (C. H. Johnson, personal observation).

No studies to date have focused on explanations for the northward dispersal of the species beyond Cape Hatteras. The common occurrence of this species south of Massachusetts and the large amount of small boat traffic, especially recreational, passing along the eastern seaboard suggest that specimens of *B. neritina* would have dispersed north on occasion as mentioned by

Winston and Hayward, but failed to become permanent residents until sometime in the last decade. One possible explanation for why the environment is now suitable for stable colonization by *B. neritina* in Massachusetts may be linked with the change in coastal water temperatures over the past decade. Long term records of sea surface temperature taken at Woods Hole document an upward trend beginning around 1960 (S. W. Nixon, S. Granger, B. A. Buckley, M. Lamont and B. Rowell, 'A one hundred and seventeen year coastal water temperature record from Woods Hole, Massachusetts', *Estuaries* 27 (3) (2004) 397-404). By 2007, it is possible that the local water temperature at Woods Hole reached a level suitable for establishment of *B. neritina*.

In a study covering the period of 2006 to 2012 of fouling bryozoans in Eel Pond and adjacent regions, Johnson and colleagues (C. H. Johnson, J. E. Winston, and R. M. Woollacott, 'Western Atlantic introduction and persistence of the marine bryozoan *Tricellaria inopinata*', *Aquatic Invasions* 7 (3) (2012) 295-303) found in a collection from September 2010 another arborescent bryozoan, *Tricellaria inopinata*. This species is common in European waters, but had not previously been reported from the western Atlantic. Specimens were not present in any preceding survey and specifically not in July of that year. Those individuals that over-wintered began regrowth late in May 2011 and began reproduction in early June. From the 2011 season to the present, *T. inopinata* remains the dominant erect bryozoan in this fouling community. Three factors apparently contribute to its success in the Eel Pond fouling community: *T. inopinata* begins reproduction earlier than the former dominant species, *B. stolonifera*, and thereby gains an advantage in colonizing space available early in the season; *T. inopinata* settles on and overgrows resident species; larvae of other species do not settle on colonies of *T. inopinata*.

- 79 B.H. Grave, 'Rate of growth, age at sexual maturity, and duration of life of certain sessile organisms, at Woods Hole, Massachusetts', *Biological Bulletin* 65 (3) (1933) 375-386 [Life history of *B. flabellata* on p. 384].
- 80 B.H. Grave, '*Bugula flabellata* and *B. turrita*', in P.S. Galtsoff et al. (eds.), *Culture Methods for Invertebrate Animals*, Comstock, Ithaca, NY (1937) 178-179.
- 81 F. Ormes, note 44.
- 82 C.P. Hickman, note 53.
- 83 W.E. Edington, note 43.
- 84 'Clark Grave', *American Civil War Soldiers*, online database by Historical Data Systems, Kingston, MA, found through <http://Ancestry.com>, accessed 10 October 2012.
- 85 *The Minnesota Alumni Weekly* 19(1) 29 September (1919) 39; 'Field Operations', *The Medical Department of the United States Army in the World War*, 8 (1925) 466-468.
- 86 Caswell was a captain in the Chemical Warfare Service, Trench Warfare Branch Design Section, Washington, DC. Thomas Brooks Grave held the rank of private in the Chemical Warfare Service. *Maryland in the World War 1917-1919*, 1, Maryland War Records Commission, Baltimore (1933) 792.
- 87 U.S. Selective Service System, 'Benjamin Harrison Grave', World War I Draft Registration Cards 1917-1918, Illinois, Knox County, Draft Board 2, 12 September 1918; U.S. Selective Service System, 'Benjamin Harrison Grave', Selective Service Registration Cards World War II, Fourth Registration, Indiana, Putnam County, 27 April 1942.
- 88 Hamm, Thomas D., 1988, *The Transformation of American Quakerism: Orthodox Friends, 1800-1907*, Bloomington, Indiana University Press, 261 pp.
- 89 B.H. Grave to L. Grave, 28 December 1924, Letters between Lucy, Grace, Willard, Anna and

- Mary Thorne Moore, 1893-1954, Moore and Grave family correspondence, Earlham College Archives.
- 90 Caswell Ph.D. in Zoology 1899, Benjamin Ph.D. in Zoology 1910, Thomas H. enrolled 1905-06 (no degree), Floyd MD 1914. W. Norman Brown, 1926, note 10.
- 91 In the 1910 census, Caswell is listed as the head of household, with his wife Josephine, their son Thomas B., and Caswell's brothers Benjamin and Thomas H. Grave residing together. *Thirteenth Census of the United States, 1910*, Baltimore Ward 13, Baltimore (Independent City), Maryland; Roll: T624_557, pg: 3B, Enumeration District 0197.
- 92 *Earlham Press*, Richmond, Indiana, 14 June 1916 p. 4; *ibid*, 6 January 1917 p. 4; *ibid* 26 April 1919 p. 3; *ibid* 8 January 1921 p. 3; *ibid* 3 December 1923 p. 3; *ibid* 2 June 1931 p. 3; *ibid* 9 May 1933 p. 1.
- 93 After graduating from Earlham College in 1895, Caswell Grave entered graduate school at Johns Hopkins University where he came under the mentorship of W. K. Brooks, who was to later influence Caswell's brother Benjamin in selection of the latter's dissertation topic. Caswell Grave's dissertation concerned the larval development of a brittle star and was accepted in typescript form on May 10, 1899 (W.K. Brooks and C. Grave, '*Ophiura brevispina*.', in *Memoirs of the National Academy of Sciences*, Vol. VIII, Fourth Memoir, Government Printing Office, 1899 [Introductory note by W. K. Brooks: "As my name appears upon the title-page of this memoir, it is proper for me to state that my share in the work has been that of the instructor under whose direction the work has been done. The discovery that this ophiuran is of peculiar interest and that it is unusually favorable for the study of the problems of the morphology of Echinoderms, was made by Dr. Grave; and the results which are here detailed are his work."])). Caswell Grave remained on the faculty of Johns Hopkins University until 1919 when he moved to Washington University in St. Louis, Missouri, where he would spend the remainder of his career. While at Washington University he is credited with building the biology department to one of the most influential of its time in the country. He spent summer holidays at U. S. Commission of Fish and Fisheries laboratories, first at Woods Hole, Massachusetts, and later at Beaufort, North Carolina. He was director of the Beaufort lab from 1902 – 1906. While at Beaufort, Grave became interested in the biology of oysters and from 1906 to 1912 was shellfish commissioner for the State of Maryland. Caswell Grave devoted many summers to the Marine Biological Laboratory at Woods Hole as an instructor, investigator and trustee and later at the Carnegie Laboratory at the Dry Tortugas in Florida. In this latter stage of his career Grave became interested in the study of ascidians, focused especially on the initiation of metamorphosis of the ascidian tadpole larva (S.O. Mast, 'Caswell Grave January 24, 1870-January 8, 1944', *Science* 99 (2566) (1944): 174-175).
- 94 O.S. Strong, 'The Chemical Room: its Past and Present', *The Collecting Net* 2 (4) 1927, 4-5. T.B. Grave graduated from Johns Hopkins University with a Ph.D. in Chemistry in 1923.
- 95 *The DePauw*, note 50.
- 96 L. Grave to Mrs Packard, October 1936; W.C. Dennis to B.H. Grave, 21 December 1936, Moore and Grave family correspondence, Earlham College Archives.
- 97 C.P. Hickman, Jr., note 48; F. Ormes, note 44.
- 98 Certificate of Death of Benjamin H. Graves [sic], Marion County Health Department, Indianapolis, Indiana.
- 99 F. Ormes, note 44.
- 100 W.E. Edington, note 43.
- 101 Mary Louise Reynolds, personal communication, 29 May 2013.

Appendix 1. Publications of Benjamin Harrison Grave

Publications (Excluding Abstracts)

- B.H. Grave, 1942. The sexual cycle of the shipworm, *Teredo navalis*. *Biological Bulletin* **82**(3), 438-445.
- B.H. Grave, 1937a. *Bugula flabellata* and *B. turrita*, pp. 178-179. In P.S.Galtsoff et al.(eds.) *Culture Methods for Invertebrate Animals*. Comstock, Ithaca, NY.
- B.H. Grave, 1937b. *Nereis limbata*, pp. 182-184. In P.S.Galtsoff et al.(eds.) *Culture Methods for Invertebrate Animals*. Comstock, Ithaca, NY.
- B.H. Grave, 1937c. *Hydroides hexagonus*, pp. 185-187. In P.S.Galtsoff et al.(eds.) *Culture Methods for Invertebrate Animals*. Comstock, Ithaca, NY.
- B.H. Grave, 1937d. *Chaetopleura apiculata*, pp. 519-520. In P.S.Galtsoff et al.(eds.) *Culture Methods for Invertebrate Animals*. Comstock, Ithaca, NY.
- B.H. Grave, 1937e. *Cumingia tellinoides*, pp. 543-545. In P.S.Galtsoff et al.(eds.) *Culture Methods for Invertebrate Animals*. Comstock, Ithaca, NY.
- B.H. Grave, 1937f. Rearing *Teredo navalis*, pp. 545-546. In P.S.Galtsoff et al.(eds.) *Culture Methods for Invertebrate Animals*. Comstock, Ithaca, NY.
- B.H. Grave and J. Smith, 1936. Sex inversion in *Teredo navalis* and its relation to sex ratios. *Biological Bulletin* **70**(2), 332-343.
- B.H. Grave, 1934. Further studies on the longevity and swimming ability of spermatozoa. *Biological Bulletin* **67**(3), 513-518.
- B.H. Grave, 1933. Rate of growth, age at sexual maturity, and duration of life of certain sessile organisms, at Woods Hole, Massachusetts. *Biological Bulletin* **65**(3), 375-386. [Life history of *B. flabellata* on pg. 384]
- B.H. Grave, 1932. Embryology and life history of *Chaetopleura apiculata*. *Journal of Morphology* **54**(1), 153-160.
- B.H. Grave, 1931. The Amphibia of Montgomery County, Indiana. *Proceedings of the Indiana Academy of Science* **40**, 339.
- B.H. Grave, 1930. The natural history of *Bugula flabellata* at Woods Hole, Massachusetts, including the behaviour and attachment of the larva. *Journal of Morphology* **49**(2), 355-384.
- B.H. Grave and J.F. Oliphant, 1930. The longevity of unfertilized gametes. *Biological Bulletin* **59**(2), 233-239.
- B.H. Grave, 1928a. Natural history of shipworm, *Teredo navalis*, at Woods Hole. *Biological Bulletin* **55**(4), 260-282.
- B.H. Grave, 1928b. Vitality of the gametes of *Cumingia tellinoides*. *Biological Bulletin* **54**(5), 351-362.
- B.H. Grave and R.C. Downing, 1928. The longevity and swimming ability of spermatozoa. *Journal of Experimental Zoology* **51**(3), 383-388.
- B.H. Grave, 1927a. An analysis of the spawning habits and spawning stimuli of *Cumingia*

- tellinoides*. *Biological Bulletin* **52**(6), 418-435.
- B.H. Grave, 1927b. The natural history of *Cumingia tellinoides*. *Biological Bulletin* **53**(3), 208-219.
- B.H. Grave, 1922. An analysis of the spawning habits and spawning stimuli of *Chaetopleura apiculata* (Say). *Biological Bulletin* **42**(5), 234-256.
- B.H. Grave, 1917. *Zeugophora scutellaris* (Suffr.). *Journal of Morphology* **30**(1), 245-259.
- B.H. Grave and E.P. Walker, 1916a. Wyoming birds and their value to agriculture. *University of Wyoming Bulletin* **12**(6), 1-137.
- B.H. Grave and E.P. Walker, 1913 [1916b]. *The Birds of Wyoming with an explanation of recent changes in their distribution, economic aspects also considered*. University of Wyoming, Laramie, Wyoming, 137 p. [1913 is printed on the cover, but an author's note from 1916 states that printing was delayed and post-1913 data added. Grave preferred this title over the edition published as a University of Wyoming Bulletin.]
- B.H. Grave, 1914. *Laboratory Guide for a Course in Invertebrate Zoology*. Cadmus Press, Galesburg, Illinois. 113 p.
- B.H. Grave, 1913. The influence of the development of agriculture in Wyoming upon the bird fauna. *American Naturalist* **47**(557), 311-313. [Author's name misprinted as B.H. Grove.]
- B.H. Grave, 1912. The otocyst of the Pinnidae. *Biological Bulletin* **24**(1), 14-17.
- B.H. Grave, 1911. Anatomy and physiology of the wing-shell *Atrina rigida*. *Bulletin of the Bureau of Fisheries* **29**, 409-439, pls. XLVIII-L. [Published version of Grave's Ph.D. dissertation]
- B.H. Grave, 1909a. *Pinna seminuda*. *Johns Hopkins University Circulars* **6**, 46-51.
- B.H. Grave, 1909b. Some observations on the habits of *Pecten dislocatus*. *Biological Bulletin* **16**(5), 259-264.

Abstracts

- B.H. Grave, 1942. The sexual cycle in *Teredo navalis*. *Proceedings of the Indiana Academy of Science* **51**, 265.
- B.H. Grave, 1932. Further studies on the longevity and swimming ability of spermatozoa. *Anatomical Record* **54**(3, Supplement), 24.
- B.H. Grave, 1929a. Behavior of the larva of *Bugula flabellata*. *Anatomical Record* **44**(3), 198.
- B.H. Grave, 1929b. Periodicity in spawning by *Cumingia tellinoides*. *Anatomical Record* **44**(3), 198.
- B.H. Grave and J.F. Oliphant, 1929. The longevity of unfertilized gametes. *Anatomical Record* **44**(3), 199. [Oliphant's initials are misprinted as J.K. Oliphant in the original.]
- B.H. Grave, 1924. Rate of growth and age of sexual maturity of certain sessile organisms. *Anatomical Record* **29**(2), 90.

Unpublished Works

- B.H. Grave, 1910. Anatomy and physiology of *Atrina (Pinna) rigida* (Dillwyn). 67 p. [Typescript of Ph.D. dissertation, Johns Hopkins University.]
- B.H. Grave, 1906. The Development of the Microspore and Megaspore in *Lilium tigrinum*. [M.S. thesis, Carleton College.]
- B.H. Grave, n.d. The Destiny of Man. 49 p. [Incomplete draft document. Typescript donated to Earlham College Archives by Bartram Cadbury (Grave's nephew), 1997.]

Appendix 2. Marine invertebrate species published on by Benjamin Harrison Grave

Journal articles and contributions to an edited volume, but excluding published abstracts. No attempt has been made in compiling this list to update the taxonomic status of the species studied by Grave.

Annelida - Polychaeta

Chaetopleura apiculata 1922, 1932, 1937*Hydroides hexagonus* 1930, 1933, 1937*Nereis limbata* 1937

Arthropoda - Crustacea

Balanus eberneus 1933

Bryozoa - Gymnolaemata

Bugula flabellata 1930, 1933, 1937*Bugula turrita* 1930, 1937

Chordata - Urochordata - Ascidiacea

Botryllus gouldii 1933*Molgula manhattensis* 1933

Cnidaria - Hydrozoa

Campanularia calceolifera 1933*Campanularia flexuosa* 1933*Gonothyrea loveni* 1933*Obelia commissuralis* 1933

Echinodermata- Echinoidea

Arbacia punctulata 1928, 1934

Mollusca – Bivalvia

Atrina rigida 1911, 1912

Cumingia tellinoides 1927a, 1927b, 1928, 1928b, 1933, 1934, 1937

Pecten dislocatus 1909

Pinna nobilis 1912

Pinna seminuda 1909a

Pinna sp. (unidentified small red *Pinna* from Jamaica)

Teredo navalis 1928a, 1933, 1936, 1937, 1942

