

Perspectives

Anecdotal, Historical and Critical Commentaries on Genetics

Thomas Hunt Morgan at the Marine Biological Laboratory: Naturalist and Experimentalist

Diana E. Kenney and Gary G. Borisy¹

Marine Biological Laboratory, Woods Hole, Massachusetts 02543

IN the early 1910s, researchers at the Marine Biological Laboratory (MBL) in Woods Hole, Massachusetts, might have wondered why a colleague, Thomas Hunt Morgan (Figure 1), began shipping fruit flies from his Columbia University lab to the MBL each summer. After all, the Woods Hole currents supplied the MBL with a rich variety of marine organisms and Morgan, an avid practitioner of experimental embryology, made good use of them.

Yet those who knew Morgan well would not have been surprised by his insect stocks. A keen naturalist, Morgan studied a veritable menagerie of experimental animals—many of them collected in Woods Hole—as a student and later researcher at the MBL from 1890 to 1942. Moreover, Morgan always had a diversity of investigations going on simultaneously. “This was the way Morgan worked: he wasn’t happy unless he had a lot of different irons in the fire at the same time,” wrote A. H. Sturtevant, Morgan’s long-term collaborator (STURTEVANT 2001, pp. 4–5). In Morgan’s first 3 decades at the MBL, for instance, he studied at least 15 different species, including the now-famous fruit fly, while investigating a variety of problems related to his central interests in development and heredity (MORGAN 1888–1937; MARINE BIOLOGICAL LABORATORY 1909).

Morgan was also a vocal proponent of experimentalism, and at the MBL he (quite successfully) joined with Jacques Loeb in arguing for a quantitative, predictive foundation for biological studies (ALLEN 1969). Morgan was interested only in scientific problems that could be experimentally tested. Deeply wary of ungrounded hypotheses, he sought not overarching theories, but experimental methods that would allow him to identify proximate causes. This stance would triumph in Morgan’s work with the fruit fly, *Drosophila melanogaster*.

Morgan initially began breeding this animal in his search for an experimental approach to evolution: he was testing an alternative to the theory of natural selection, which he felt was insufficient to explain the origin of new species. But when a sex-linked mutation appeared in his Columbia University stocks in 1910, Morgan’s attention was diverted to analyzing the material basis of sex determination and inheritance. By 1912, he and his colleagues were mapping the location of genes on chromosomes. These epoch-making studies launched the field of experimental genetics.

Morgan’s penchant for maintaining multiple, diverse lines of investigation paid off in important ways, as this review of his work at the MBL up through the mid-1920s shows. First, Morgan was able to synthesize his research on many different organisms in his book *Regeneration* (MORGAN 1901), which today provides a useful and insightful perspective on regenerative medicine. Second, evidence from originally distinct studies conceptually converged for Morgan. An example is his post-1910 work at the MBL on the insects phylloxeran and aphid, which confirmed his early *Drosophila* results on the relationship of the chromosomes to sex determination and inheritance.

Morgan’s dual characteristics as a “naturalist and experimentalist” (Figure 2) place him historically in an era when biology was transitioning from a descriptive and often speculative field to an experimental one (ALLEN 1969). Yet they may indicate also why Morgan was a successful scientist, one who received the first Nobel Prize ever awarded in genetics in 1933 and became the first in a now-long list of Nobel Laureates affiliated with the MBL. Morgan’s appreciation of natural diversity and his wide-ranging investigations, coupled with his skepticism toward *a priori* theories, could have left him flailing in a biological wilderness. What anchored him was his strict experimentalism, his insistence on choosing problems that could be analytically tested.

¹Corresponding author: Office of the Director, Marine Biological Laboratory, 7 MBL St., Woods Hole, MA 02543.
E-mail: gborisy@mbl.edu

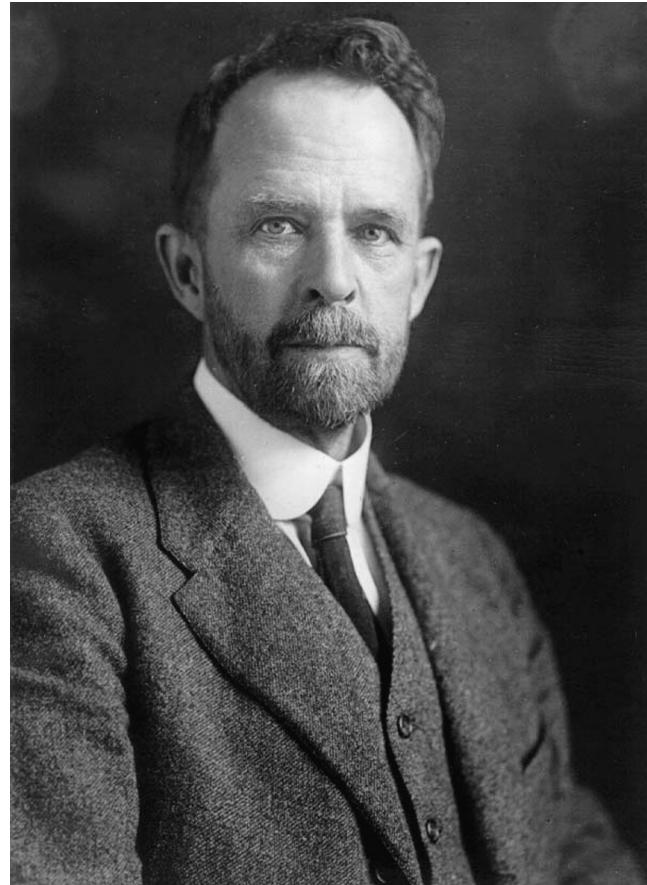


FIGURE 1.—T. H. Morgan in 1920. This portrait of Morgan was taken by A. F. Huettner. Courtesy of MBL Archives.

EARLY YEARS: MARINE ORGANISMS, MORPHOLOGY, AND EXPERIMENTAL EMBRYOLOGY

In 1886, when T. H. Morgan was 20 years old and about to start graduate studies in zoology at Johns Hopkins, he attended the summer marine laboratory in Annisquam, Massachusetts, where he first learned how to collect and handle marine organisms for basic biological research. “Altogether, I am delighted with myself for being here and without doubt the work will be of the greatest assistance to me next winter,” he wrote to a friend (ALLEN 1978, p. 25). As it turned out, the Annisquam laboratory closed down after that summer, and its benefactors moved its glassware, apparatus, boats, furniture, and fixtures to Woods Hole, where they established the MBL in 1888 (LILLIE 1944). When Morgan died in 1945, he was “the last surviving personal link” between the MBL and its predecessor at Annisquam, wrote Edwin G. Conklin of Princeton University, Morgan’s close friend and 45-year colleague at the MBL (CONKLIN 1947, p. 14).

At Johns Hopkins, Morgan trained with embryologist W. K. Brooks, who promoted the use of marine organisms for studies of early development, as was then practiced at the Naples Zoological Station and other

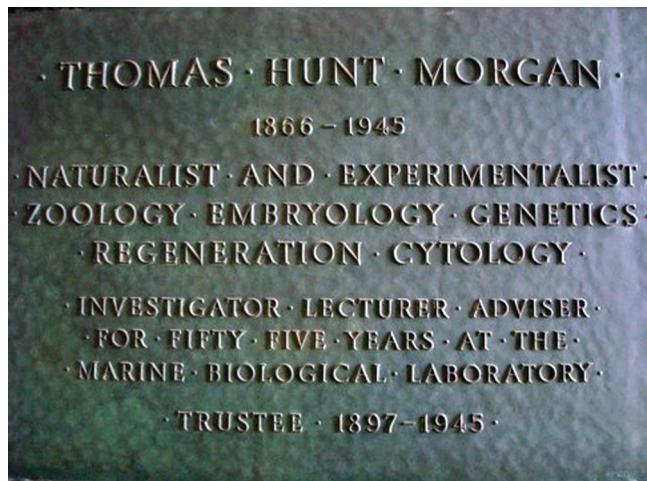


FIGURE 2.—Naturalist, experimentalist, and trustee. This plaque in the lobby of Lillie Laboratory at the MBL commemorates T. H. Morgan’s long-term and wide-ranging activities at the laboratory. Courtesy of Matthew Person.

European marine laboratories. Through Brooks’ arrangement, Morgan spent the summer of 1889 at the U.S. Fish Commission Laboratory in Woods Hole, and the following summer Morgan was one of 20 investigators at the nascent MBL, which had opened in 1888. During these two summers, Morgan collected and studied sea spiders for his doctoral research. Morgan, like Brooks, was then working within the paradigm of descriptive morphology; in his thesis, he sought to trace the phylogenetic relations of sea spiders with other arthropods by studying their embryological development. In 1891, after defending his thesis and accepting an assistant professorship at Bryn Mawr College, Morgan returned to the MBL and did so again for the next two summers.

Morgan’s activities in those years are not much noted in descriptions of the MBL written by his contemporaries. Yet Morgan’s profile in Woods Hole rose significantly after he spent 10 months at the Naples Zoological Station in 1894–95, carrying out research with the German embryologist Hans Driesch. Through Driesch, Morgan came into direct contact with the European school of experimental embryology that had begun in the 1870s with Wilhelm His, who developed methods for sectioning embryos and argued for a cleaving of the field from phylogenetic studies. Morgan had already been attracted to these new methods and this approach and had devised experiments on teleost and echinoderm eggs at the MBL in 1893. Other MBL investigators were interested, too. A few months before Morgan left for Naples, W. M. Wheeler translated Wilhelm Roux’s manifesto for an experimental and mechanistic approach to embryology, or *Entwicklungsmechanik*, and presented it as a Friday Night Lecture at the MBL (ROUX 1895; MAIENSCHEN 1991).

Morgan's Naples experiments, which were designed to identify causal factors controlling development of the egg cell, made a singular impression on his Woods Hole contemporaries. Edmund B. Wilson, Morgan's longtime friend and colleague at Columbia University and at the MBL, described a "beautiful experiment" Morgan conducted in Naples in which he manipulated the relative position of frog blastomeres and gave "most conclusive evidence that each of the (first) two blastomeres contains all the materials, nuclear and cytoplasmic, necessary for the formation of a whole body, and that these materials may be used to build a whole body or half-body, according to the grouping that they assume" (MORGAN 1895; WILSON 1897, p. 319). In another experiment, Driesch and Morgan showed with ctenophore eggs that if part of the cytoplasm is removed, the remainder gives rise to incomplete larvae showing defects corresponding to the part removed (DRIESCH and MORGAN 1895). "Thus the way was prepared for theories of organ-forming germ regions in the egg and later of 'organ-forming substances,'" wrote Frank R. Lillie in his history of the MBL. "The chapter in experimental embryology that immediately follows from this is a long one, with important contributions from Woods Hole investigators," particularly Wilson, Conklin, Lillie, and Morgan himself (LILLIE 1944, p. 128).

REGENERATION AND ARTIFICIAL PARTHENOGENESIS: FROM EARTHWORMS TO SEA URCHINS

After his Naples stay, Morgan next returned to the MBL as an investigator in 1897. At that point, he also became deeply involved in organizational matters at the MBL and was named a trustee, a position he would hold for the rest of his life (CONKLIN 1947). Over the next five years, Morgan's research interests at the MBL would dovetail closely with those of Jacques Loeb, whom MBL director C. O. Whitman had recruited to establish a department of physiology at the MBL in 1894. Loeb had also been influenced by Driesch and was even more adamant than Morgan in his experimentalist, mechanistic approach to biology. Together, Morgan and Loeb waged battle in Woods Hole against the descriptive, phylogenetic tradition. "Loeb has been here [in Woods Hole] . . . all summer and I have learned to know him so much better," Morgan wrote to Driesch in 1899. "We agree on so many fundamental views (and differ on these points from most of the people here) that we have become very good friends and strong allies. We have done battle with nearly all the other good morphologists and still survive their united assaults" (ALLEN 1978, p. 326).

The first line of research Loeb developed at the MBL was regeneration (LILLIE 1944). Morgan, beginning in 1897, also pursued experiments on regeneration in a variety of organisms, including earthworms, hermit

crabs, and teleost fish. By 1901 he had published more than 30 articles and a book on the topic, and much of this work was carried out at the MBL (MARINE BIOLOGICAL LABORATORY 1909; MAIENSCHEN 1991). Morgan saw regeneration as essentially similar to normal development; he understood the value of using regenerative organisms to study both. One outcome of Morgan's extensive studies on regeneration was they led him to initially reject the Darwinian theory of natural selection, particularly the idea that adaptations have arisen due to their usefulness. How could the regenerative power have been slowly acquired through selection, Morgan argued, since it is useful to the animal only if the injured part entirely regenerates in a single generation? "The building up of the complete regeneration by slowly acquired steps, that cannot be decisive in the battle for existence, is not a process that can be explained by the theory (of natural selection)," he wrote (MORGAN 1901, p. 129). These considerations would lead Morgan to explore alternative mechanisms for the origin of species, which later led to his experimental use of fruit flies.

In 1899, Morgan was at the front lines of Jacques Loeb's spectacular discovery of artificial parthenogenesis at the MBL, which brought the lab much publicity (LOEB 1899). Morgan reported in 1896 and in 1898 on the induction of artificial asters in sea urchin eggs by the use of hypertonic seawater and in 1899 on the effects of various salt solutions on unfertilized sea urchin eggs, finding that they caused irregular cell division (MORGAN 1896, 1898, 1899). These latter experiments, carried out at the MBL, nearly "come to a complete anticipation of Jacques Loeb's famous discovery," Lillie wrote (LILLIE 1944, p. 133). According to A. H. Sturtevant, later Morgan's long-term collaborator, there was "at the time a rather general feeling that Loeb had taken more credit than was due him for his discovery of artificial parthenogenesis," and Morgan "clearly felt that Loeb had been secretive about his own work and had used every opportunity to find out just what Morgan was doing"; however, Morgan "was not as resentful as were some other members of the Woods Hole group on his behalf" (STURTEVANT 1959, p. 288). The artificial parthenogenesis episode seems not to have unduly troubled Morgan; he and Loeb remained friendly until Loeb's death in 1924.

SEX DETERMINATION: INSECT STUDIES

Beginning about 1906, Morgan also pursued studies of sex determination in insects at the MBL, focusing on phylloxerans and on aphids that he later reported collecting from bearberry plants at nearby Quissett, Massachusetts (MORGAN 1915). The relationship of the chromosomes to sex determination was at that time a topic of vigorous investigation at the MBL, particularly by Thomas H. Montgomery, Edmund B. Wilson, and Nettie Stevens, a former student of Morgan's at Bryn

Mawr (MARINE BIOLOGICAL LABORATORY 1909). Parallel cytological studies by Wilson and Stevens in 1905 (not at the MBL) provided strong evidence that the X chromosome determined sex, but Morgan remained unconvinced, believing the cytoplasm and physiological development played a more important role.

The evolution of Morgan's thought on sex determination is apparent in his papers on the phylloxerans and aphids, both of which have a life-cycle phase in which parthenogenetic eggs produce both males and females. Morgan wanted to find out what in the egg determines what sex it will become. In 1906, Morgan reported finding no discernible difference between the chromosomes of the male-producing and the female-producing phylloxeran eggs, nor in their cytoplasm. In watching them develop, though, he noted one important difference: "the precocious development of the relatively enormous reproductive organs of the male," suggesting that "a pre-existing mass of cytoplasm from which the testis develops may be present in the egg." This led him to suggest that "the immediate determination of the sex is a cytoplasmic phenomenon" (MORGAN 1906, p. 206). In 1908, he reported having discovered that somatic cells in the female phylloxeran have six chromosomes, while those in the male have only five; thus at some point in the parthenogenetic egg the ones that will become male lose a chromosome. He was still considering cytoplasmic influences: "It follows that the egg as well as the sperm has the power of determining sex by regulating the number of its chromosomes," he wrote (MORGAN 1908, p. 57). In a 1909 study of both phylloxerans and aphids, Morgan concluded that the sex of the egg is determined to be male or female before any change in chromosome number. "Clearly, the egg as well as the sperm contains factors that determine sex," he wrote (MORGAN 1909, p. 235).

Then, an event in Morgan's *Drosophila* research, which he had initiated in about 1908, catalyzed a distinct change of course in his thought. In May 1910, Morgan discovered a male fly with a white-eyed mutation in his *Drosophila* stocks at Columbia University. By June, he had done enough crosses to realize he had in his white-eyed fly "a splendid case of sex-limited inheritance," as he wrote to a friend from Woods Hole (SCHWARTZ 2008, p. 179). Morgan submitted his classic Science paper describing his new *Drosophila* results from Woods Hole, and it was published in July (MORGAN 1910). Although Morgan described the expression of the white-eyed mutation in males only, it is noteworthy that he did not mention chromosomes in this paper. Yet Morgan soon found additional sex-linked traits in *Drosophila*, which he first publicly reported in a lecture at the MBL in July 1910. These findings would lead him to accept the chromosomal theory of sex determination, as well as chromosomes serving as the physical basis for Mendelian inheritance (MORGAN 1911a; ALLEN 1978; MAIENSCHEN 1984). In 1912, after his *Drosophila* discoveries and with new cytological evidence from the phylloxerans, Morgan

unequivocally ascribed differences in the male and female parthenogenetic phylloxeran eggs to differences in their sex chromosomes. (Prior to this, he admitted in this paper, "the value of the chromosome hypothesis in sex determination" might have seemed to "hang in the balance.") (MORGAN 1912, p. 479).

Sturtevant considered Morgan's phylloxeran and aphid work, which he continued to pursue in Woods Hole until 1915, as very important in confirming the chromosome hypothesis. "[Morgan] showed that the facts, which at first seemed quite inconsistent with the chromosome interpretation of sex determination, were in fact intelligible only in terms of that interpretation," Sturtevant wrote. "This was one of Morgan's most brilliant achievements, involving great skill and patience in the collecting and care of the animals, insight in seeing what were the critical points of study, and ability to recognize and to follow up on unexpected facts. The results were of importance in serving to demonstrate the role of the chromosomes in sex determination, at a time when that importance was seriously questioned by many biologists" (STURTEVANT 1959, pp. 289–290).

MENDEL AND MUTATIONS: MICE AND FRUIT FLIES

The rediscovery of Gregor Mendel's work in 1900 brought questions of evolution and heredity to the fore in biological circles. Morgan began investigations of Mendelian inheritance in 1905, when he started breeding rats and mice (KOHLER 1994). In the summer of 1907, he caught a house mouse in Woods Hole with the "sport," or mutation, of a pure white belly. "Later, I caught two more such mice and, in the same closet, another typical house mouse. In the neighborhood, I have caught a few other white-bellied mice," Morgan reported (which summons a vision of an agile Morgan chasing mice around Woods Hole). Morgan then obtained white-bellied mice from Iowa and New York and began a series of breeding experiments crossing the wild sport with various domesticated races. "My intention was to familiarize myself at first hand with the process of Mendelian inheritance," he wrote, by observing the varieties of coat color that his crosses produced (MORGAN 1911b, p. 88).

At some point in the midst of this work, probably in 1908, Morgan started breeding *Drosophila*, not for Mendelian studies, but as a foray into experimental evolution. Morgan's studies of regeneration had led him to reject Darwin's concept of new species arising by natural selection of minute, random, continuous variations. Instead, Morgan entertained Hugo de Vries' concept that species evolved through discrete jumps, which de Vries called mutations (ALLEN 1978). De Vries had predicted that, under certain conditions, animals can enter "mutating periods." With *Drosophila*, Morgan wanted to see if he could induce such a mutating period through intensive inbreeding (ALLEN 1975; KOHLER 1994).



FIGURE 3.—Morgan and friends: T. H. Morgan called this photo, taken at the MBL in the summer of 1919, “Solving the Problems of the Universe.” Clockwise from left: T. H. Morgan, Calvin Bridges (kneeling), Franz Schrader, E. E. Just, A. H. Sturtevant, and an unidentified person. Courtesy of MBL Archives.

The first researchers to use *Drosophila* experimentally were William E. Castle and his students at Harvard University (CASTLE *et al.* 1906) and Morgan was clearly influenced by this work. It is not certain who gave Morgan his first *Drosophila* stocks; but “certainly some of the early material was collected in grocery stores which existed then in Woods Hole,” Sturtevant wrote (STURTEVANT 2001, p. 3). Morgan himself in a letter to A. F. Blakeslee in 1935, responding to whether he had obtained his first stocks of flies from F. E. Lutz, wrote “...if so, I have forgotten it” (CARLSON 2004, p. 168).

For many months, Morgan’s inbreeding experiments with *Drosophila* turned up nothing, and when Ross Harrison visited Morgan’s Columbia University lab in January 1910, Morgan referred to it as “two years’ work wasted” (KOHLER 1994, p. 41). Yet, soon after, a stream of mutants began appearing in his stocks, starting with an atypical thorax pattern. Overjoyed, Morgan at first thought he had succeeded in inducing a de Vriesian mutating period in the fly (KOHLER 1994). But soon the sex-limited Mendelian ratios Morgan observed for white-eye and other mutations drew his attention from his original focus on experimental evolution to an analysis of the chromosomes in sex determination and inheritance, despite his prior skepticism toward the chromosomal theory. As Castle later wrote, “Morgan was too good a scientist to hold a conclusion after he believed it had been clearly disproved” (CARLSON 2004, p. 163).

Beginning in 1913 and continuing through the 1920s, Morgan brought members of his Columbia University “fly room,” particularly A. H. Sturtevant and C. B. Bridges, to the MBL each summer, where they carried out their *Drosophila* research in the Crane Building

(STURTEVANT 1959) (Figure 3). “This did not mean any interruption in the *Drosophila* experiments,” Sturtevant later wrote. “All the cultures were loaded into barrels—big sugar barrels—shipped by express, and what you started in New York, you’d finish (in Woods Hole) and vice versa.” They traveled from New York by boat, lugging cages of chickens, pigeons, mice, and other animals Morgan was working on, and “when Morgan got to Woods Hole, he plunged deeply into work on marine forms, even while his work with *Drosophila* was actively going on,” Sturtevant wrote (STURTEVANT 2001, p. 4). From 1917 to 1924, for example, Morgan conducted an extended study of regeneration and “intersex” mutations in the fiddler crab at the MBL (MORGAN 1920, 1924). Also accompanying Morgan to Woods Hole since their marriage in 1904 was biologist Lilian Vaughan (Sampson) Morgan, who investigated amphibian breeding and development at the MBL in the 1890s and later transitioned into genetics. In 1913, Lilian Morgan cofounded what is now the Children’s School of Science in Woods Hole (KEENAN 1983).

Morgan’s success with *Drosophila* in establishing a material basis for the Mendelian theory of inheritance was a triumph of the experimentalist approach, which would come to dominate biological research in the 20th century. Yet the diversity of Morgan’s studies at the MBL over more than 50 years indicates he also appreciated the naturalist Louis Agassiz’s dictum, which is still displayed in the MBL Library: “Study Nature, not Books.” In Morgan’s time, the naturalist and the experimentalist traditions seemed to pose a dichotomy: descriptive *vs.* quantitative, holistic *vs.* reductionistic. Morgan did not choose either/or: he adopted, with great success, something of both.

The authors are grateful to Jane Maienschein and Garland E. Allen for helpful discussions about Morgan and for generously providing feedback and suggestions on the manuscript. The authors also thank Catherine N. Norton, library director, and Diane M. Rielinger, archivist, of the Marine Biological Laboratory Woods Hole Oceanographic Institution Library, Woods Hole, Massachusetts, for archival assistance.

LITERATURE CITED

- ALLEN, G. E., 1969 T. H. Morgan and the emergence of a new American biology. *Q. Rev. Biol.* **44:** 168–188.
- ALLEN, G. E., 1975 The introduction of *Drosophila* into the study of heredity and evolution, 1900–1910. *Isis* **66:** 322–333.
- ALLEN, G. E., 1978 *Thomas Hunt Morgan: The Man and His Science*. Princeton University Press, Princeton, NJ.
- CARLSON, E. A., 2004 *Mendel’s Legacy: The Origin of Classical Genetics*. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY.
- CASTLE, W. E., F. W. CARPENTER, A. H. CLARK, S. O. MAST and W. M. BARROWS, 1906 The effects of inbreeding, cross-breeding, and selection upon the fertility and variability of *Drosophila*. *Proc. Am. Acad. Arts Sci.* **41:** 729–786.
- CONKLIN, E. G., 1947 Thomas Hunt Morgan: 1866–1945, in The Marine Biological Laboratory, forty-ninth report, for the year 1946. *Biol. Bull.* **93**(1): 14–18.

- DRIESCH, H., and T. H. MORGAN, 1895 Zur analysis der ersten entwicklungstadien des ctenophoreneis. I. Von der entwicklung einzelner ctenophorenblastomeren; II. Von der entwicklung ungefurchter eier mit protoplasmadefekten. Arch. Entwicklungsmech. **2**: 204–226.
- KEENAN, K., 1983 Lilian Vaughan Morgan (1870–1952): her life and work. Am. Zool. **23**: 867–876.
- KOHLER, R. E., 1994 *Lords of the Fly: Drosophila Genetics and the Experimental Life*. University of Chicago Press, Chicago.
- LILLIE, F. R., 1944 *The Woods Hole Marine Biological Laboratory*. University of Chicago Press, Chicago.
- LOEB, J., 1899 On the nature and process of fertilization and the production of normal larvae (plutei) from the unfertilized eggs of the sea urchin. Am. J. Physiol. **3**: 135–138.
- MAIENSHEIN, J., 1984 What determines sex: a study of converging approaches, 1880–1916. Isis **75**: 456–480.
- MAIENSHEIN, J., 1991 *Transforming Traditions in American Biology, 1880–1915*. The Johns Hopkins University Press, Baltimore.
- MAIENSHEIN, J., 1991 The origins of entwicklungsmechanik, pp. 43–61 in *A Conceptual History of Modern Embryology*, edited by S. F. GILBERT. The Johns Hopkins University Press, Baltimore.
- MARINE BIOLOGICAL LABORATORY, 1909 The 11th annual report of the Marine Biological Laboratory, years 1907–1908. Biol. Bull. **17**: 56–100.
- MORGAN, T. H., 1888–1937 *Collected Reprints of T. H. Morgan, 1888–1937*. MBL Library Archives, Woods Hole, MA.
- MORGAN, T. H., 1895 Half-embryos and whole-embryos from one of the first two blastomeres of the frog's egg. Anat. Anz. **10**: 623–628.
- MORGAN, T. H., 1896 The production of artificial astrophores. Arch. Entwicklungsmech. Org. **3**: 339–361.
- MORGAN, T. H., 1898 The effect of salt-solutions on unfertilized eggs of Arbacia. Science **7**: 222–223.
- MORGAN, T. H., 1899 The action of salt-solutions on the unfertilized and fertilized eggs of Arbacia, and of other animals. Arch. Entwicklungsmech. Org. **8**: 448–539.
- MORGAN, T. H., 1901 *Regeneration*. MacMillan, New York.
- MORGAN, T. H., 1906 The male and female eggs of phylloxerans of the hickories. Biol. Bull. **10**: 201–206.
- MORGAN, T. H., 1908 The production of two kinds of spermatozoa in phylloxerans—functional ‘female producing’ and rudimentary spermatozoa. Soc. Exp. Biol. Med. Proc. **5**: 56–57.
- MORGAN, T. H., 1909 Sex determination and parthenogenesis in phylloxerans and aphids. Science **29**: 234–237.
- MORGAN, T. H., 1910 Sex limited inheritance in Drosophila. Science **32**: 120–122.
- MORGAN, T. H., 1911a An attempt to analyze the constitution of the chromosomes on the basis of sex-limited inheritance in Drosophila. J. Exp. Zool. **11**: 365–413.
- MORGAN, T. H., 1911b The influence of heredity and of environment in determining the coat colors of mice. Ann. NY Acad. Sci. **21**: 81–117.
- MORGAN, T. H., 1912 The elimination of the sex chromosomes from the male-producing eggs of phylloxerans. J. Exp. Zool. **12**: 479–498.
- MORGAN, T. H., 1915 The predetermination of sex in phylloxerans and aphids. J. Exp. Zool. **19**: 285–321.
- MORGAN, T. H., 1920 Variations in the secondary sexual characters of the fiddler crab. Am. Nat. **54**: 220–246.
- MORGAN, T. H., 1924 The artificial induction of symmetrical claws in male fiddler crabs. Am. Nat. **58**: 289–295.
- ROUX, W., 1895 The problems, methods and scope of developmental mechanics, pp. 149–190 in *Biological Lectures Delivered at the Marine Biological Laboratory*, translated by W. M. WHEELER (in 1894). Ginn and Co., Boston.
- SCHWARTZ, J., 2008 *In Pursuit of the Gene*. Harvard University Press, Cambridge, MA.
- STURTEVANT, A. H., 1959 Thomas Hunt Morgan, 1866–1945. Biogr. Mem. Natl. Acad. Sci. **33**: 283–325.
- STURTEVANT, A. H., 2001 Reminiscences of T. H. Morgan. Genetics **159**: 1–5.
- WILSON, E. B., 1897 *The Cell in Development and Inheritance*. MacMillan, London.