Studies in Spermatogenesis (1905), by Nettie Maria Stevens [1]

By: Cox, Troy Keywords: chromosomal sex determination [2]

Studies in Spermatogenesis is a two volume book written by Nettie Maria Stevens, and published by the Carnegie Institution of Washington [3] in 1905 and 1906. In the books Stevens explains the research she conducted on chromosomal sex determination [4] in the sperm [5] and egg [6] cells of insect species while at Bryn Mawr College [7], near Philadelphia, Pennsylvania. *Studies in Spermatogenesis* described early examples of chromosomal XY sex determination [8].

Studies in Spermatogenesis described research on the generation of sperm [5] cells (spermatogenesis) and their role in the fertilization [9] of egg [6] cells. Like much of the work conducted in genetics at the beginning of the 1900s, Stevens's research was influenced by two events at the turn of the twentieth century. The first was the rediscovery of Gregor Mendel's theories of inheritance in the late 1890s that revitalized the field of genetics. Mendel, who worked in Europe in the mid nineteenth century, developed a law of heredity that provided a framework to explain how a parent could transfer traits to its offspring, even though researchers couldn't describe the the genetic materials that carried these traits. From 1902 to 1903 Walter Sutton at Columbia University [10] in New York, New York and Theodor Boveri [11] in Würzburg, Germany independently worked to identify this unknown genetic material. Sutton and Boveri concluded that chromosomes, the rod-shaped structures located inside the nucleus [12] of every cell, are the genetic material of inheritance, providing a matter for Mendel's Laws.

Prior to Stevens's work, two theories emerged to explain sex determination [4]. The first attributed the effect to environmental conditions, which according to some researchers caused the developmental fates of the embryo. The second ascribed sex determination [4] to the internal factors of organisms, such as the cytoplasm or nucleus [12] of the egg [6]. Stevens's research was part of the internalist approach, and she focused on chromosomal differences in sperm [5] cells. Stevens's research on the chromosome contained in sperm [5] cells stemmed from research on accessory chromosomes conducted a few years earlier by Clarence Erwin McClung, a former teacher of Sutton, at the University of Kansas [13] in Lawrence, Kansas.

In 1902 McClung published "The Accessory Chromosome–Sex Determinant?" In this article, McClung theorized that an odd number of chromosomes found in insects [14] from some species formed a basis of sexual determination [8] by which an extra chromosome caused cells to differentiate differently than normal. McClung's hypothesis influenced Stevens's work as each insect she studied for *Studies in Spermatogenesis* was observed to either verify or refute the presence of the extra chromosome. Although Stevens did not find extra chromosomes in her work with aphids in 1904, Stevens held that the sperm [5] and the eggs somehow determined the sex of an offspring.

Studies in Spermatogenesis has two parts. Part I, published in 1905, begins with a reference to McClung's theory of accessory chromosomes and states the need to further investigate the theory as a potential sex determination [4] mechanism. Stevens next introduces five insects [14] previously unstudied for sex determination [4]: termite (*Zootermopsis angusticollis* [15]), sand cricket (*Stenopelmatus* [16]), German cockroach (*Blattella germanica* [17]), mealworm (*Tenebrio molitor* [18]), and aphid [19] (*Aphis oenotherae* [20]). Stevens describes the methods used to microscopically view the testes [21] of each insect. Stevens details her results for the individual stages of spermatogenesis and for the presence or absence of accessory chromosomes for each insect. The results also reference figures that are present at the end of the book, providing visual representations of the results. Stevens concludes each section with a summary of the important observations made for each particular insect. Part I concludes with a general discussion of each insect in relation to McClung's hypothesis and reiterates the importance of the findings in *Tenebrio molitor*, namely that in both somatic and sex cells, one particular chromosome was smaller in male cells than the corresponding chromosome in female cells.

In Part II of *Studies in Spermatogenesis*, published in 1906, Stevens further discusses her studies on XY sex determination [4]. Stevens focuses on beetles, specifically the species *Tenebrio molitor*. Stevens searched for similar sexual differentiation [22] mechanisms in species similar to *T. molitor* to confirm sex determination [4] by a distinct chromosomal element. She identifies nineteen species belonging to eight different families in which sex determination [4] is identified by a small chromosomal element similar to *T. molitor*.

Stevens devotes a much of *Studies in Spermatogenesis* to her work with the mealworm by describing both the germ cells [23] (precursor cells to egg [6] and sperm [5] cells) and the somatic cells of mealworms. At the time, researchers had noted that somatic cells contained a number of chromosomes, with one half contributed by each parent. They had also noted that germ cells [23] contained half of the number chromosomes found in somatic cells. In mealworms, Stevens found ten large chromosomes in eggs and either ten large or nine large and one small chromosome in the spermatocytes, which later mature

into sperm [5] cells. Stevens also describes the somatic cells of mealworms as containing twenty large chromosomes in females, and nineteen large and one small chromosome in males. After repeatedly observing that the comparatively small chromosomes were present only in male somatic and germ cells [23], Stevens concluded that an egg [6] fertilized by a male sex cell (spermatozoon) that contains the small chromosome will develop into a male. Likewise, an egg [6] fertilized by a spermatozoon containing the larger chromosome will develop into a female.

Studies in Spermatogenesis influenced biologists such as Edmund Beecher Wilson [24] and Thomas Hunt Morgan [25], two of Stevens's mentors at Bryn Mawr College [7]. In 1905, Wilson, a professor of Zoology at Columbia University [10], published "Studies on Chromosomes" in which he describes a form of XY and X0 sex determination [4]. However, Wilson remained skeptical about attributing sex to a particular type of chromosome until further information supported the theory. Wilson suggested instead that the intensity of chromosomes varied between sexes and that environmental causes could affect their intensity. After Stevens published her results in September 1905, Wilson revised his previous publications, deleting references to environmental influences. Instead, Wilson cited Stevens's work as supporting his original theories.

Studies in Spermatogenesis provides one of the first observations of XY sex determination [8]. Stevens's findings allowed researchers to locate the material of Mendelian inheritance that passed specific traits, in this case the sex of the organism *Tenebrio molitor*, through a distinct chromosomal element.

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Subject

Spermatogenesis [37] Stevens, N. M. (Nettie Maria), 1861-1912 [38] Sex determination, Genetic [39] Sex differentiation [40] Embryos [41] Developmental biology [42] Sex chromosomes [43] McClung, C. E. (Clarence Erwin), 1870- [44] Wilson, Edmund B. (Edmund Beecher), 1856-1939 [45] Morgan, Thomas Hunt, 1866-1945 [46] Sex Determination Processes [47]

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