Ernest Everett Just, PhD: Pioneer in Ecological Developmental (Eco-Devo) Biology

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Ernest Everett Just, a pioneering American biologist, discovered the fundamental role of the environment in the development of embryos. His work led to the creation of the area of biology known as ecological developmental (Eco-Devo) biology. However, both his work and the context of his scientific contributions are not widely known. His work covered a diversity of fields of biology, including marine biology, cytology, and parthogenesis (asexual reproduction where growth and development of embryos occur without fertilization). His findings provided important concepts in developmental biology that are used to this day. Specifically, he demonstrated the importance of the cellular cytoplasm and ectoplasm, in addition to the nucleus, in determining how development occurs in embryos. His worked was unique for its use of in vivo conditions using a variety of marine organisms. His publications on the "***Basic Methods for Experiments on Eggs of Marine Mammals"*** in 1922 and "***The Biology of the Cell Surface***" in 1939 are still regarded as two of the most comprehensive reviews in cell biology. In this manuscript we present Dr. Just's childhood in Charleston, SC, unlikely attendance and success at Dartmouth College, and his groundbreaking work, which was developed at the Marine Biological Laboratory (MBL) at Woods Hole, Europe, and Howard University.

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Early Years

Ernest Everett Just was born August 14, 1883 on Inspection Street in Charleston, South Carolina, the first of three children of Charles and Mary Just (Figure 1). His father, a wharf builder, died when Just was only four years old in 1887, leaving his mother as the sole provider. She sold off the house at 28 Inspection Street to pay off creditors and moved from Charleston to James Island three miles away[1]. Here she worked in the phosphate mines, which produced phosphate used as a commercial fertilizer cheap enough to sustain farming after the Civil War[1]. Mary invested her earnings in real estate, purchasing several hundred acres adjacent to Charleston in an area known as the "Hillsborough Plantation"[1]. Here she persuaded the habitants of this settlement to form a town, which was then named after her-Maryville[1]. At the time, this was one of the first African-American governments in the state[1]. The illiteracy rate was high, because few teachers could be induced to teach in such a rural environment[1], so Mary dedicated the next 10 years of her life teaching children, including Ernest[1]. His mother's dedication to teaching affected Ernest deeply[1]. Ernest attended her school until the summer of 1896, when Mary felt he had reached the limits of what her school could offer. Mary then sent him to the South

Figure 1. Memorial in Charleston, South Carolina at the birth site of Ernest Evertt Just (present day).

Carolina State College, part of an African-American high school and college in Orangeburg, South Carolina about 60 miles away, which she funded herself. Here he was placed in a four year curriculum to be trained as a teacher, which he finished in three[1]. Upon returning to Maryville after graduating, Mary had Ernest consider attending the Kimball Union Academy in Meriden, New Hampshire, which she had read about in the *Christian Endeavor World*, one of her few outside sources of information[1].

Formal Education

At the age of 17, Just applied to, and was accepted by, the Kimball Union Academy in Meriden, NH; however, he could not afford the ticket to travel north. To earn his way, Just worked aboard a Clyde Line steamship[2]. Once the ship arrived in New York, Just worked for a month before going to New Hampshire[2]. While at Kimball Union Academy, Just was editor of the school paper and president of the debating society of this predominantly Caucasian school. He wanted to attend Bowdoin College in New Brunswick, MA, to further his education, but his teachers persuaded him to attend Dartmouth College[2]. There, he studied English, Biology, and History, and graduated in 1907 *magna cum*

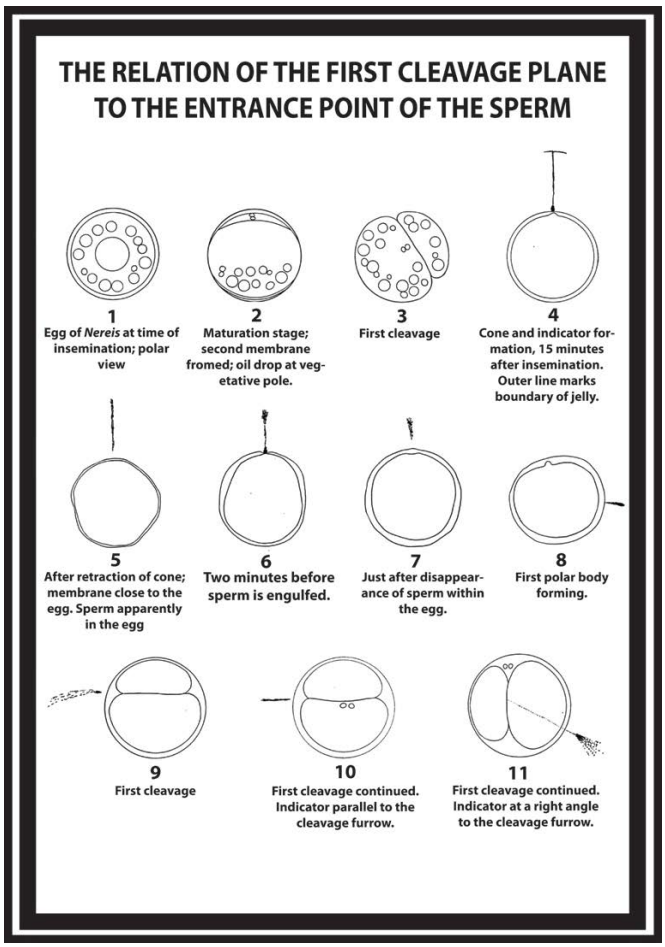

Figure 2. *The Relation of the First Cleavage Plane to the Entrance Point of the Sperm*. These compiled hand drawings of an overview of the changes in cell surface following fertilization of the egg cell from the marine polychaete worm *Nereis* were produced and published by Ernest Just in 1912, providing evidence for the importance of theories supporting the role of germinal areas in the cytoplasm[14]. Used with permission.

laude as a Rufus Choate scholar. Just also was elected to the Phi Beta Kappa society and received honors in botany and sociology, and special honors in history, zoology, and English[3].

The Professor and the Scientist

In the fall of 1907, Just began work as a faculty member in the English Department at Howard University in Washington, DC, with an annual salary of $400 [1]. He taught sociology, logic, and dramatics[4]. In 1909, Just began his graduate training at the Marine Biological Laboratory (MBL) in Woods Hole, MA with a course in marine invertebrates, and then, in 1910, a course in embryology. That same year, Howard University built the Thirkield Science Hall to increase the science faculty and Just was asked to teach zoology[4,5]. His dedication to the English Department made him hesitate in taking on this new task, but, a salary increase to $1,000 annually induced him to accept this offer[2]. Soon after, Just became the first Head of the Zoology Department and, with a grant from the Rosenwald Foundation, started a Master's program in zoology[5]. This grant allowed Just to conduct research for six months during the year, and totaled over $80,000; it was renewed in 1928[2]. While at MBL, one of Just's former Dartmouth biology professors referred him to Frank R. Lillie at the University of Chicago. He acted as a research assistant to Lillie between 1911 and 1912 doing work on a paper on *Platynereis megalops* (a marine annelid worm) fertilization. This work was the basis for Just's Ph.D. thesis[3,5], entitled "Studies of Fertilization in *Platynereis megalops*," which was completed in 1915. Since he was a dedicated professor at Howard University, Just's completion of his PhD was delayed[3].

In 1912, Just published his first scientific paper, *The Relation of the First Cleavage Plane to the Entrance Point of the Sperm* (Figure 2). Even though this was his first paper, the results were significant as he showed "that the sperm entry point determines the first cleavage plane in the egg of *Nereis* (polychaete worm, including the sandworm) and *Platynereis* (marine annelid worm) as well as *Echinarachnius* (common sand dollar) fertilization reactions[5]. Due to his early success and research productivity, Just had already published six papers prior to receiving his Ph.D. in 1916[6-10]. Just produced well over 50 papers all with one common theme: the cell nucleus is not the only structure that is responsible for heredity, as the cytoplasm and ectoplasm influence the nucleus so all structures share equal responsibility[11].

The Marine Biological Laboratory at Woods Hole

The Marine Biological Laboratory (MBL) at Woods Hole, MA was founded on March 20th, 1888 as a "sea-side laboratory for instruction and investigation in biology," catering to the needs and interests of students and scientists throughout the United States[1]. The Women's Education Association had established the MBL as a coeducational laboratory, and, from its inception, women served on the MBL Board of Trustees[1]. During the summer, women investigators from large universities, like the University of Chicago and the University of Pennsylvania, would travel to MBL to conduct research. From 1909 to 1930, Just would spend all of his summers, with the exception of two, conducting research at MBL. It was here that Just first was introduced to fertilization and cell cleavage. His duties included laboratory equipment maintenance, marine specimen collection, as well as monitoring experiments. As Lillie's research assistant, Just not only conducted research but was enrolled as a student in several zoology courses, including marine invertebrates and embryology.

Just's work on marine eggs and their fertilization processes enabled him to receive his first research support, prior to earning his Ph.D., from the National Research Council (NRC). Just would maintain this funding for future studies at MBL over the next several years[1]. Just's contributions cover several areas, including the role of environmental factors in development, the fast and slow blocks to polyspermy during fertilization (i.e. how eggs prevent more than one sperm from entering), embryo morphogenesis, and experimental parthenogenesis, a form of female asexual reproduction where embryo growth and development occur without fertilization by a male. He was also very interested in the importance of the cell surface in the fertilization process, and how well laboratory conditions corresponded to the natural setting. He is considered the creator of ecological-developmental (Eco-Devo) biology, the study of development in the natural environmental context instead of the typical laboratory setting[5].

Prior to modern advances in molecular biology, scientists proposed multiple theories to explain the molecular mechanisms governing fertilization. In 1899, while Just was still at Kimball Academy, Jacques Loeb, a world renowned physiologist, demonstrated that pricking unfertilized sea urchin eggs and frog eggs with a needle, or by changing the salt concentration of the seawater in which they were cultured, induced their development[12]. Loeb proposed his lysin theory, which postulated that sperm carried a molecular substance, or a cytolyzer he termed lysin, that activated the egg to promote development in the book entitled *Artificial Parthenogenesis and Fertilization*[1]. However, while many biologists applauded Loeb's efforts for stimulating research in biology at the molecular level, many felt his approach was too simplistic. Lillie was among the scientists who felt there was a more extensive mechanism involved in fertilization. In 1906, Lillie published a comprehensive paper on his fertilizin theory[13], which proposed that fertilization relied on biochemical interaction of substances, the major one being fertilizin, carried by the sperm and egg. Lillie's theory proposed that there were three essential elements: the sperm, the egg and a substance secreted by the egg that reacts with both egg and sperm[13]. He argued that fertilizin caused sperm agglutination in the same species. He further proposed the concept of receptors, suggesting that spermatozoa were unable to bind directly to the egg, requiring ferilizin to act as a receptor between the two, based on Ehrlich's conceptions of a 'side chain' theory of antibodies[13].

Lillie's theory marked the importance of cell surface physiology in the fertilization process, which was the basis of Just's graduate research. From 1911 - 1912, Just extensively explored fertilization and breeding habits in the marine worms *Nereis* and the sea-urchin *Arbacia*. In his first paper, "The Relation of the first Cleavage Plane to the Entrance Point of the Sperm" published in 1912[14], Just used an ingenious method to show that the plane of symmetry in development is determined by the polar bodies and the point of entrance of the spermatozoon. Just would further observe the fertilization process in marine invertebrates, resulting in publication of papers on the breeding habits of the marine worms *Nereis limbata* and *Platynereis megalops*[9,10]. Just's laborious, yet superb, efforts in specimen collection and observation put him in a favored position at the MBL. Other investigators admired him as a scientist with firsthand experience with marine specimens. Each year, Just would arrive a Woods Hole earlier than he did the year before, and, in some cases, would not return to Howard until a day or two prior to his classes starting[1].

Biology of the Cell Surface

After receiving his Ph.D. in 1916, Just continued to characterize the cell surface. In one of his most innovative studies, he exposed *Echinarachnius parma* (the common sand dollar) eggs to dilute seawater at different time points following insemination and measured the position of membrane separation relative to the point of sperm-egg fusion and the time it took for each egg to rupture at this position[15]. This study uncovered how the zygote surface moves in a wave from the point of the sperm entry to the opposite side, thus demonstrating that the envelope forms as a result of structural changes at the egg surface[15].

In 1928, while in Europe, Just began to develop his theory on the importance of the ectoplasm, the outer, non-granulated part of the cytoplasm, in development. In 1932, Just lectured at the International Congress of Zoologist, held in Padua, Italy where he presented his newly proposed theory for the first time[26]. He subsequently published three articles on the subject: "Der Rolle des kortikalen Cytoplasmas bei vitalen Erscheinungen" (The role of cortical cytoplasm in vital phenomena") in the German journal Naturwissenschaftern, and two articles in the *American Naturalist,* "On the Origin of Mutations" and "Cortical Cytoplasm and Evolution"[16-18]. He believed that the ectoplasm linked the environment and an animal's nature, affecting reactions, shape and conditioning. Just found support in work completed by German biologist J.A. Hammar, who also insisted on the importance of the ectoplasm and was a supporter of Lillie's theory of fertilizin, a substance believed to associate with the ectoplasm[13].

Early in his career, Just proposed the concept of fast blocks to polyspermy, by which the eggs of sexually reproducing organisms inhibit successful penetration by subsequent sperm after fertilization[16], caused by a shift in egg cell membrane potential[5]. This process occurs in many different animal species, but sea urchins are the most widely studied[19]. Unfertilized sea urchin eggs have an internal negative charge, which becomes positive upon fertilization. This electrical polyspermy block occurs because a positively charged molecule in the sperm surface membrane is repelled by the positive charge at the egg surface[20]. Just also sought experimental evidence to support his mentor Frank Lillie's fertilizin theory of fertilization. This would lead to the publication of a long defense titled, "*The Present Status of the Fertilizin Theory of Fertilization*", which demonstrated that this process occurred in a variety of marine animals[21,22]. In 1939, Just's book, titled *The Biology of the Cell Surface*[23], served as a thorough overview of his theory of the ectoplasm, while also displaying his many years of extensive hands-on research. Although to some, his work may appear more philosophical, Just provided grounded methodology and techniques that further supported the numerous examples from his own experimental studies.

Studies Abroad

In Europe, Just's work was considered far-reaching and was very well received. He was elected to honorary societies in France, appointed to the editorial boards of German journals, and was invited to speak at numerous conferences all over Europe, including Berlin, Budapest and Rome[1]. However, Just could not attend these meetings due to a lack of funding. In 1928, after tireless persistence on Just's behalf, the Julius Rosenwald Fund awarded a grant to fund the Department of Biology of Howard University in the amount of $80,000.00 over a five-year period[1]. At the time, no other black scientist had ever achieved such a substantial level of funding[1]. The award provided funds for Just's student Roger Arliner Young to train at the MBL. Most importantly, this new funding provided Just with funding to travel overseas and, for the next five years, Just would immerse himself in, and come to love, European culture. In early January 1929,

filled with a new sense of purpose, Just boarded the *Dresden* in New York Harbor and set sail for Europe[1].

In the years prior to his first departure for Europe, Just had experienced a great deal of prejudice in America. Although Just received numerous research grants, none could compensate for his failure to receive an appointment in a large university or research institute, where faculty members were often not as distinguished as himself. In addition, tensions developed at the MBL, and Just never felt fully accepted there. His teaching and administrative duties at Howard University, coupled with a low level of university support, often kept him out of the laboratory, preventing him from conducting the level of research he had envisioned. Frustrated and embittered by his treatment in his native land, Just believed that Europe could provide more opportunities for him. He would travel to Europe repeatedly over the next eight to nine years, sometimes staying for as long as two years. He conducted most of his research at the Stazione Zoologica in Italy, the Kaiser-Wilhelm Institut für Biologie in Berlin, Germany, and at the Station Biologique in France[1].

Those years abroad not only brought about a change in Just's professional life, but also his personal life. Just had married Ethel Highwarden on June 12, 1912, who taught German at Howard University. They subsequently had three children: Margaret, Highwarden, and Maribel. While in Germany, Just had the first of his affairs with Margret Boveri, a secretary at the Kaiser-Wilhelm-Institut and the daughter of the German biologist Theodor Boveri [24], who was known for a number of key discoveries, including that the presence of all chromosomes are necessary for proper embryonic development, the phenomenon of chromatin diminution during development, and the concept that cancers result from chromosome damage leading to uncontrolled cell division. Later, in 1931, Just met Hedwig Schnetzler who became his companion and later his wife[24]. Once officials took note of both the affair and the inter-racial nature of the affair, he was asked to leave. In 1939, he divorced his wife of twenty-seven years to marry Dr. Hedwig Schnetzler, a white German biologist who once served as his assistant at the Kaiser-Wilhelm-Institut[1]. The couple would later have a daughter named Elisabeth.

Spingarn Medal

Ernest Just was an American scientist devoted solely to conquering the complexities of the egg surface during fertilization. His observations and conclusions remains a vital component of modern day courses in development. As a dedicated teacher and mentor, Just substantially upgraded research quality and medical training at Howard University. In 1915, Just was selected by the NAACP (National Association for the Advancement of Colored People) for the first Spingarn Medal ever awarded. The award was established in 1914 by J.E. Spingarn, the chairman of the NAACP executive committee, to honor a man or woman of African descent and American citizenship who, during the year, had made the highest achievement in any field of human endeavor. The award was conferred in the Ethical Culture Hall in New York City, on February 12, 1915, by New York Governor Charles Seymour Whitman[2]. Just was very modest about winning the award, stating, "I was at first anxious because I am jealous for high standards. I really felt my work measured by of grade among zoologists is paltry and that the Association might do far better to honor some more well known worker."[4] Despite his hard work and continuous efforts in biological research, Just felt he had not yet contributed substantially enough to his field. He would express his sincere gratitude to the NAACP in a 1922 letter stating, "It seems to me that the primary value of the Spingarn medal lies in this direction - that it can serve as an inspiration and goal. Certainly, I can now thank you most heartily for what the medal has meant to me, although at the time I was really anxious to get out of receiving it. I doubt if I can make you appreciate how much of a consecration the award was"[4].

Conclusions

In June of 1940, Just's health began to fail due to complications from pancreatic cancer. At the same time, the Nazis seized control of Paris and surrounding areas. Just was detained and briefly imprisoned, but, with the assistance of friends, was soon released. He intended to reside permanently in Europe, but was forced to return to the United States due to the war[2]. In the fall of 1941, Just and his wife returned to the United States by escaping through Portugal[25]. Just settled in Washington, D.C., once again, taking up residence with his sister Inez, a nurse. Just returned to Howard University for the 1940 - 1941 academic year. His salary was $5000, almost half what he received under the Rosenwald and Carnegie grants he previously held[1]. Despite a directive from Howard University president Mordecai Johnson, ordering him to return to the classroom, Just was bedridden and too sick to move. On Monday morning, October 27, 1941, Just lost his battle with cancer and died[1].

Just's untimely death was felt by the whole science community. His mentor, Dr. Frank Lillie, published a heartfelt obituary outlining Just's scientific contributions[3]. He is remembered still as a founding member of the internationally known Omega Psi Phi Fraternity, the first African-American national fraternal organization to be founded at a historically black college. Several universities, including Howard University and the Medical University of South Carolina (MUSC), celebrate his memory by hosting symposia in his honor. In the days leading up to his death, Just made two very memorable donations, one for $25 to the Kimball Union Academy, the preparatory school he attended in South Carolina, and the other for $100 to Dartmouth College[1]. Dartmouth College has established an E. E. Just Professorship in Natural Sciences, held by Dr. George Langford for many years. There is also a thriving E. E. Just Club at Dartmouth College, for mentoring and recruiting minority students into science[25]. Though Just's life was affected seriously by racial and personal complications, his experimental studies have demonstrated lasting value as a testament to his scientific excellence.

Notes and references

Note: *KMW and BAW contributed equally to this publication.*

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