Endoderm [1]

By: MacCord, Kate Keywords: mesendoderm [2]

Endoderm is one of the germ layers—aggregates of cells that organize early during embryonic life and from which all organs and tissues develop. All animals, with the exception of sponges, form either two or three germ layers [3] through a process known as gastrulation [4]. During gastrulation [4], a ball of cells transforms into a two-layered embryo made of an inner layer of endoderm [5] and an outer layer of ectoderm [6]. In more complex organisms, like vertebrates, these two primary germ layers [3] interact to give rise to a third germ layer, called mesoderm [7]. Regardless of the presence of two or three layers, endoderm [5] is always the inner-most layer. Endoderm forms the epithelium—a type of tissue in which the cells are tightly linked together to form sheets—that lines the primitive gut. From this epithelial lining of the primitive gut, organs like the digestive tract, liver, pancreas, and lungs develop.

Throughout the early stages of gastrulation [4], a group of cells called mesendoderm expresses sets of both endoderm [5]- and mesoderm [7]-specific genes [8]. Cells in the mesendoderm have the ability to differentiate into either mesoderm [7] or endoderm [5], depending upon their position among surrounding cells. Scientists have found mesendoderm is widespread among invertebrates, including the nematode *Caenorhabditis elegans* [9], and the purple sea urchin [10], *Strongylocentrotus purpuratus* [11]. Within vertebrates, mesendoderm has been found in the zebrafish, *Danio rerio* [12], and has been indicated in mice, *Mus musculus* [13].

Endoderm, along with the other two germ layers [3], was discovered in 1817 by Christian Pander, a doctoral student at the University of Würzburg [14], in Würzburg, Germany. In his dissertation, *Beiträge zur Entwickelungsgeschichte des Hühnchens im Eie* (*Contributions to the Developmental History of the Chicken in the Egg*), Pander described how two layers give rise to a third in the chick [15] (*Gallus gallus* [16]) embryo. Pander's description of the formation of these layers is the first account of gastrulation [4] in the chick [15], and it grounded future studies of the germ layers [3]. Martin Rathke at the University of Königsberg, in Königsberg, Prussia (later Poland), soon found evidence in a developing crayfish [17], *Astacus astacus* [18], of the two layers Pander had described. Rathke's finding marked the first discovery of endoderm [5] and ectoderm [6] in an invertebrate, but that information was not further investigated for two decades.

The germ layers [3] drew the attention of many scientists in the nineteenth century. Karl Ernst von Baer [19] at the University of Königsberg, extended the concept of germ layers [3] to include all vertebrates in his 1828 text *Über die Entwickelungsgeschichte der Thiere. Beobachtung und Reflexion* (*On the Developmental History of the Animals. Observations and Reflections*). Twenty years later, natural historian Thomas Henry Huxley [20], in England, applied Pander's concept of germ layers [3] to jellyfish. In his 1849 paper "On the Anatomy and Affinities of the Family of the Medusae," Huxley noted that the two layers of cells he saw in the adult jellyfish related to each other the same way as the germ layers [3] in chick [15] embryos described by Pander. The association that Huxley made between the body plan of the adult jellyfish and the vertebrate embryo connected the study of growth and development, called ontogeny [21], to the study of relationships between organisms, called phylogeny [22]. Huxley's support for a relationship between ontogeny [21] and phylogeny [22], later known as the theory of recapitulation, would become fundamental to the works of late nineteenth century scientists, like Charles Darwin [23], in England, and Ernst Haeckel [24] at the University of Jena [25], in Jena, Germany. These and other scientists began to look to embryos for evidence of evolution [26].

By the 1860s researchers compared germ layers [3] across the animal kingdom. Beginning in 1864 embryologist Aleksandr Kovalevsky, who studied embryology [27] at the University of St. Petersburg, in St. Petersburg, Russia, studied invertebrates. His research showed that invertebrate embryos had the same primary germ layers [3], endoderm [5] and ectoderm [6], as vertebrate embryos, and that the layers arose in the same fashion across the animal kingdom. Kovalevsky's findings convinced many about the universality of the germ layers—a result that some scientists made a principle of germ layer theory. Germ layer theory held that each of the germ layers [3], regardless of species, gave rise to a fixed set of organs. These organs were deemed homologous across the animal kingdom, effectively uniting ontogeny [21] with phylogeny [22]. Scientists like Haeckel in Germany and Edwin Ray Lankester [28] at the University College [29], London, in London, England convinced many to accept germ layer theory by the end of the nineteenth century.

While germ layer theory garnered broad support, not everyone accepted it. Beginning in the late nineteenth century, embryologists such as Edmund Beecher Wilson [30], in the United States, and Wilhelm His [31] and Rudolf Albert von Kölliker [32], both in Germany, objected to the absolute universality of the germ layers [3] that the theory demanded. These opponents of germ layer theory belonged mainly to a new tradition of embryologist—those who used physical manipulations of embryos to research development. By the 1920s, experiments by scientists like Hans Spemann [33] and Hilde Mangold [34], in Germany, and Sven Hörstadius, in Sweden, led scientists to dismantle the germ layer theory.

Early twentieth-century scientists sought to explain the germ layers [3] more fully by investigating how embryos transformed from one cell to thousands of cells. Among these embryologists, Edwin Grant Conklin [35] at the University of Pennsylvania [36], in Philadelphia, Pennsylvania, was one of the first to trace cell lineages from the single-cell stage. In his 1905 text *The Organization and Cell-lineage of the Ascidian Egg*, Conklin mapped the divisions and subsequent specialization of the cells in the embryo of an ascidian, or sea squirt, a type of marine invertebrate that develops a tough outer layer and clings to the sea floor. By creating a plot, or fate map, of the developmental route of each of the cells, Conklin located the precursor cells, traced the formation of each of the germ layers [3], and showed that even at very early stages of development, the ability of some cells to differentiate becomes restricted.

Conklin's fate mapping [37] experiments, along with questions about the capacity of cells to differentiate, influenced scientists like Robert Briggs, at Indiana University [38] in Bloomington, Indiana, and his collaborator, Thomas King, at the Institute for Cancer Research [39] in Philadelphia, Pennsylvania. In the 1950s Briggs and King began a series of experiments to test the developmental capacity of cells and embryos. In 1957 Briggs and King transplanted nuclei from the presumptive endoderm [5] of the northern leopard frog [40], *Rana pipiens* [41], into eggs from which they had removed the nuclei. This technique, which Briggs and King helped create, called nuclear transplantation [42], allowed them to explore the timing of cell differentiation [43], and the technique became a basis for future experiments in cloning [44]. From their nuclear transplantation [42] experiments, Briggs and King found that during endodermal differentiation [43], the ability of the nucleus [45] to help cells specialize becomes progressively restricted. That result was supported in 1960 by the work of John Gurdon [46], at Oxford University in Oxford, England. Gurdon recreated Briggs and King's experiments using the African clawed frog [40], *Xenopus laevis* [47], and Gurdon found that there are significant differences between species in the rate and timing of onset of these endodermal restrictions.

While Briggs, King, and Gurdon worked to understand the restriction of endodermal cell fates, other scientists, like Pieter Nieuwkoop, at the Royal Netherlands Academy of Arts and Science, in Utrecht, Holland, investigated the formation of the germ layers [3]. In 1969 Nieuwkoop published an article, "The Formation of the Mesoderm in Urodelean Amphibians. I. Induction by the Endoderm," in which he examined the interactions of the endoderm [5] and ectoderm [6]. Nieuwkoop divided embryos of the salamander [48], *Ambystoma mexicanum* [49], into regions of presumptive endoderm [5] and presumptive ectoderm [6]. When left to develop in isolation, mesoderm [7] did not form. But when he recombined the two tissues, the endoderm [5] induced the formation of mesoderm [7] in adjacent regions of the ectoderm [6].

Although scientists had traced the fate of the endoderm [5], investigated the capacity of endodermal cells to differentiate, and had examined the induction [50] potential of said cells, they did not investigate the molecular pathways that specify and pattern the endoderm [5] until the 1990s. From these studies emerged the theory that maternal signals, or developmental effects that the mother contributes to the egg [51] prior to fertilization [52], act through three main families of protein-coding genes [8] to help regulate the early differentiation [43] of endoderm [5]. These signals are proteins β-catenin, VegT, and Otx. The molecular pathways involved in later stages of endoderm [5] differentiation [43] and patterning are different across species, especially the transcription factors, or proteins that help regulate gene expression. GATA factors in particular are expressed in mesendoderm and are necessary for the endoderm [5] to differentiate. While there are some genetic elements conserved across the animal kingdom, like β-catenin, some portions of the endoderm [5] induction [50] pathway, especially signals like the proteins Nodal and Wnt, are vertebrate-specific. In 2002 Eric Davidson [53] and his colleagues at California Institute of Technology [54] in Pasadena, California, announced the full network of genes [8] that regulate the specification of endoderm [5] and mesoderm [7] in sea urchins in their paper, "A Genomic Regulatory Network for Development." Davidson confirmed that network of genes [8] in a co-authored article published in 2012.

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Endoderm is one of the germ layers-- aggregates of cells that organize early during embryonic life and from which all organs and tissues develop. All animals, with the exception of sponges, form either two or three germ layers through a process known as gastrulation. During gastrulation, a ball of cells transforms into a two-layered embryo made of an inner layer of endoderm and an outer layer of ectoderm. In more complex organisms, like vertebrates, these two primary germ layers interact to give rise to a third germ layer, called mesoderm. Regardless of the presence of two or three layers, endoderm is always the inner-most layer. Endoderm forms the epithelium-- a type of tissue in which the cells are tightly linked together to form sheets-- that lines the primitive gut. From this epithelial lining of the primitive gut, organs like the digestive tract, liver, pancreas, and lungs develop.

Subject

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