Endoderm

By: MacCord, Kate Keywords: mesendoderm

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, two additional germ layers arise 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 connected 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, a group of cells called mesendoderm expresses sets of both endoderm and mesoderm-specific genes. Cells in the mesendoderm have the ability to differentiate into either mesoderm or endoderm, depending upon their position among surrounding cells. Scientists have found mesendoderm is widespread among invertebrates, including the nematode Caenorhabditis elegans, and the purple sea urchin, Strongylocentrotus purpuratus. Within vertebrates, mesendoderm has been found in the zebrafish, Danio rerio, and has been identified in mice, Mus musculus.

Endoderm, along with the other two germ layers, was first described in 1817 by Christian Fakker, a doctoral student at the University of Würzburg.[4] In Würzburg, Germany, in his dissertation, Beiträge zur Entwicklungs geschichte des Hühnchens im Ei: Beiträge zur Entwicklungsgeschichte des Hühnchens im Ei: Contribution to the Developmental History of the Chicken in the Eggs, Fakker described how two layers gave rise to a third in the chick (Gallus gallus) embryo. Fakker’s description of the formation of these layers is the first account of endoderm in the chick[5], and it grounded future studies of the germ layers.[6] Martin Rathke at the University of Königsberg, in Königsberg, Prussia (later Poland), soon found evidence in a developing crayfish[7], Astacus astacus, of the two layers Fakker had described. Rathke’s finding marked the first discovery of endoderm[8] and ectoderm[9] in an invertebrate, but that information was not further investigated for two decades.


By the 1860s researchers compared germ layers[25] across the animal kingdom. Beginning in 1864 embryologist Aleksandr Kovalevsky, who studied embryology[26], at the University of St. Petersburg, in St. Petersburg, Russia, his research showed that invertebrate embryos had the same primary germ layers[27] and endoderm[28] 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[29], regardless of species, gave rise to fixed organs. These organs were deemed homologous across the animal kingdom, effectively uniting ontogeny[30] with phylogeny[31]. Scientists like Haeckel[32] in Germany and Edwin Ray Lankester[33] at the University College[34], 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. In the late 1890s, nineteenth-century embryologists such as Edmund Beecher Wilson[35], in the United States, and Wilhelm His[36] and Rudolf Albert von Kölliker[37], both in Germany, objected to the absolute universality of the germ layers[38] that the theory demanded. These opponents of germ layer theory belonged mainly to a new tradition of embryology—those who used physical manipulations of embryos to research development. By the 1920s, experiments by scientists like Hans Spemann[39] and Hilde Mangold[40], in Germany, and Sven Hörstadius, in Sweden, led scientists to dismantle the germ layer theory.

Early-twentieth-century scientists sought to explain how embryos transformed from one cell to thousands of cells. Among these embryologists, Edwin Grant Conklin[41] at the University of Pennsylvania[42], 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 retrieved directly and studied the cell differentiation in the cells of 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[43], and showed that even at very early stages of development, the ability of some cells to differentiate becomes restricted.


Sources

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Gastrulation: From Cells to Embryo

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