Endoderm [1]

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Endoderm is one of the germ layers—aggregates of cells that organize during early 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 [4]. During gastrulation [4], a ball of cells transforms into a two-layered embryo made of an inner layer endoderm [5] and an outer layer of ectoderm [5]. In more complex organisms, like vertebrates, these two primary germ layers invertebrate to give rise to a third germ layer, called endoderm [6]. 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, all future digestive tracts and pancreatic, liver, and ductal organs develop.

Throughout the early stages of gastrulation, a group of cells called mesendoderm expresses sets of both endoderm [5] and mesoderm [5]specific genes [36]. Cells in the mesendoderm have the ability to differentiate into either mesoderm [5] or endoderm [5], depending upon their position among surrounding cells. Scientists have found mesendoderm is widespread among invertebrates, including the nematode Caenorhabditis elegans [34], and the purple sea urchin, Strongylocentrotus purpuratus [3]. Within vertebrates, mesendoderm has been found in the zebralike Danio rerio [3], and has been indicated in mice, Mus musculus [52].

Endoder, along with the other two germ layers [5], was discovered in 1817 by Christian Pander, a doctoral student at the University of Würzburg [3], in Würzburg, Germany. In his dissertation, Beiträge zur Entwickelungsgeschichte des Hühnchens im Ei (Contributions to the Developmental History of the Chicken in the Egg), Pander described how two layers give rise to a third in the chick [40]. Pander’s concept of three germ layers [5] and the formation of germ layers [5] in vertebrates would become fundamental to the works of late nineteenth century scientists, like Charles Darwin [55], in England, and Ernst Haeckel [56] at the University of Jena [52], in Jena, Germany. These and other scientists began to look into embryos for evidence of evolution [54].

By the 1880s researchers compared germ layers [5] across the animal kingdom. Beginning in 1884 embryologist Aleksandr Kovalyevsky, who studied embryology [3] at the University of St. Petersburg, in St. Petersburg, Russia, studied invertebrates. His research showed that invertebrate embryos had the same primary germ layers [5], endoderm [5] and ectoderm [5], as vertebrate embryos, and that the layers arose in the same fashion across the animal kingdom. Kovalyevsky’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 [5], regardless of species, gave rise to a fixed set of organs. These organs were deemed homologous across the animal kingdom, effectively unifying the organisms with phylogeny [5], Huxley’s support for a relationship between ontogeny [5] and phylogeny [5], later known as the theory of recapitulation, would become fundamental to the works of late nineteenth century scientists, like Charles Darwin [55], in England, and Wilhelm His in Germany and Edwin Ray Lankester [53] at the University College [52], London, in London, England. 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 [5], and showed that even at very early stages of development, the ability of some cells to differentiate becomes restricted.

Conklin’s fate mapping [3] experiments, along with questions about the capacity of cells to differentiate, influenced scientists like Robert Briggs, abrida University [3] in Bloomington, Indiana, and his collaborator, Thomas King, at the Institute for Cancer Research [3] 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 nuclear tissue from the presumptive endoderm [3] of the northern leopard frog [46], Rana pipiens [5], into eggs from which they had removed the nuclei. This technique, which Briggs and King had developed, called nuclear transplantation [44], allowed them to experiment with the timing of cellular differentiation [5], and the technique became a basis for future experiments involving [40]. From their nuclear transplantation [44] experiments, Briggs and King found that during endodermal differentiation [6], the ability of the nucleus [21] to help cells specialize becomes progressively restricted. That result was supported in 1960 by the work of John Gurdon [52], at Oxford University in Oxford, England. Gurdon recreated Briggs and King’s experiments by using the African clawed Xenopus laevis [3], Xenopus laevis [3], and Gurdon found that there are significant differences between species in the rate and timing of onset of these endodermal restrictions.


Although scientists had traced the fate of the endoderm [5], investigated the capacity of endodermal cells to differentiate, and had examined the endoderm [5] 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 study that maternal signals, or developmental effects that the mother contributes to the genes, interact to give rise to a third germ layer, called endoderm [5]. This germ layer 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, all future digestive tracts and pancreatic, liver, and ductal organs develop.

Sources

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Subject

Endoderm [24], Embryology [25], Embryology and Development [26], Embryology and Organogenesis [27], Gastrulation [28], Germ Layers [29], Mesoderm [30], Organogenesis [31], Organogenesis (Anatomy) [32], Organs (Anatomy) [33], Tissues [34], Cell Differentiation [35], Cell Differentiation and Development [36].

Publisher

Arizona State University. School of Life Sciences. Center for Biology and Society. Embryo Project Encyclopedia.

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Format

Articles [37]

Last Modified

Wednesday, July 4, 2018 - 04:40

DC Date Accessed

Sunday, November 17, 2013 - 17:47

DC Date Available

Sunday, November 17, 2013 - 17:47

DC Date Created

2013-11-17

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