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 [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 endoderm [5] and an outer layer of ectoderm [5]. In more complex organisms, like vertebrates, these two primary germ layers [3] interact to give rise to a third germ layer, called mesoderm [5]. 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, cells are set on the path of developing into the trachea, liver, pancreas, and lungs in the embryo. Throughout the early stages of gastrulation [4], a group of cells called mesendoderm expresses sets of both endoderm [5] and mesoderm [5]—specific genes [8]. Cells in the mesendoderm have the ability to differentiate into either endoderm [5] or mesoderm [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) embryo. Pander's discovery of the germ layers [3] and his further work created a foundation for current understanding of the development of the embryo. His 1828 text Entwickelungsgeschichte des Hühnchens im Eie (Über die Entwickelungsgeschichte der Thiere. Beobachtung und Reflexion) [16], in the United States, and Wilhelm His [17] and Rudolf Albert von Kölliker [18], both in Germany, objected to the absolute universality of the germ layers [3] theory that demanded. These opponents of germ layer theory belonged mainly to a new tradition of embryology, in which the body plan of the adult organism was determined by the movements of physical manipulations of the embryo. By the 1920s, scientists like Hans Spemann [19] and Hilde Mangold [20], in Germany, and Ernst Haeckel [21] at the University of Jena [22], in Jena, Germany. These and other scientists began to look at embryos for evidence of evolution [23].

By the 1860s researchers compared germ layers [3] across the animal kingdom. Beginning in 1864 embryologist Aleksandr Kovalevsky, who studied embryology [24] 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. Kovalevsky's findings convinced many about the universality of the germ layers [3]—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 unifying theory [25] with phylogeny [26]. Scientists like Haeckel in Germany and Edwin Ray Lankester [27] at the University College [28], 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 [29], in the United States, and Ernst Haeckel [21], in Germany, and Haeckel's student in Germany, Hilde Mangold [20], 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 the capacity of cells to differentiate from one cell to thousands of cells. Among these embryologists, Edwin Grant Conklin [30] at the University of Pennsylvania [31], in Philadelphia, Pennsylvania, in the 1900s 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 [32] (Rana pipiens), into eggs from which they had removed the nuclei. This technique, which Briggs and King developed, called nuclear transplantation [33], allowed them to experiment with the timing of cell differentiation [34], and the technique became a basis for future experiments in cloning [35]. From their nuclear transplantation [33] experiments, Briggs and King found that during endoderm differentiation [34], the ability of the nucleus [35] to help cells specialize becomes progressively restricted. That result was supported in 1960 by the work of John Gurdon [36], in United Kingdom, and more extensively by King's experiments using the African clawed frog [37], Xenopus laevis [38], 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 fate, 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 Urodela Ambilibrarians. I. Induction by the Endoderm," in which he examined the interactions of the endoderm [5] and ectoderm [5], Nieuwkoop divided embryos of the salamander [39], Ambystoma mexicanum [40], into regions of presumptive endoderm [5] and presumptive ectoderm [5], and left to when to develop in isolation [40], did not form. But when he recombinated the two tissues, then endoderm [5] induced the formation of mesoderm [5] in adjacent regions of the ectoderm [5]. Although scientists had traced the fate of the endoderm [5], investigated the capacity of endodermal cells to differentiate, and had examined the endoderm [5] prior to the 1990s. From these studies emerged the theory that maternal signals, or developmental effects that the mother contributes to the egg, acted through three main families of protein-coding genes to help regulate the early differentiation [41] of endoderm [5]. These signals are proteins β-catenin, Vg1, and Ovo. The molecular pathways involved in later stages of endoderm [5] differentiation [42] 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 [5] and are necessary for gene regulation in 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 [43] pathway, especially signals like the proteins Nodal and Wnt, are vertebrate-specific. In 2006 Eric Davidson [44] and his colleagues at California Institute of Technology [45] in Pasadena, California, announced the full network of genes [46] that regulate the specification of endoderm [5] and mesoderm [5] in sea urchins in their paper, "A Genomic Regulatory Network for Development," Davidson confirmed that network of genes [46] in a co-authored article published in 2012.

Sources
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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 epiblastic lining of the primitive gut, organs like the digestive tract, liver, pancreas, and lungs develop.

**Subject**

- **Gastrulation**
- **Embryos**
- **Embryology**
- **Membranes**
- **Mesoderm**
- **Organs (Anatomy)**
- **Patterning**
- **Stem cells**

**Keywords**

- **Endoderm**
- **Mesoderm**
- **Organ formation**
- **Stem cells**

**Notes**

- 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 epiblastic lining of the primitive gut, organs like the digestive tract, liver, pancreas, and lungs develop.

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