

Germ Layers ^[1]

By: MacCord, Kate Keywords: [Germ layer theory](#) ^[2] [mesoderm](#) ^[3] [endoderm](#) ^[4] [ectoderm](#) ^[5]

A germ layer is a group of cells in an embryo that interact with each other as the embryo develops and contribute to the formation of all organs and tissues. All animals, except perhaps sponges, form two or three [germ layers](#) ^[6]. The [germ layers](#) ^[6] develop early in embryonic life, through the process of [gastrulation](#) ^[7]. During [gastrulation](#) ^[7], a hollow cluster of cells called a [blastula](#) ^[8] reorganizes into two primary [germ layers](#) ^[6]: an inner layer, called [endoderm](#) ^[9], and an outer layer, called [ectoderm](#) ^[10]. Diploblastic organisms have only the two primary [germ layers](#) ^[6]; these organisms characteristically have multiple symmetrical body axes (radial symmetry), as is true of jellyfish, sea anemones, and the rest of the phylum [Cnidaria](#) ^[11]. All other animals are triploblastic, as [endoderm](#) ^[9] and [ectoderm](#) ^[10] interact to produce a third germ layer, called [mesoderm](#) ^[12]. Together, the three [germ layers](#) ^[6] will give rise to every organ in the body, from skin and hair to the digestive tract.

Gastrulation differs across species, but the general process is the same: the hollow ball of cells that forms the [blastula](#) ^[8] differentiates into layers. The first phase of [gastrulation](#) ^[7] produces a two-layered organism comprised of [ectoderm](#) ^[10] and [endoderm](#) ^[9]. The [ectoderm](#) ^[10] will form the outer components of the body, such as skin, hair, and mammary glands, as well as part of the nervous system. Following [gastrulation](#) ^[7], a section of the [ectoderm](#) ^[10] folds inward, creating a groove that closes and forms an isolated tube down the dorsal midsection of the embryo. This process of [neurulation](#) ^[13] forms the [neural tube](#) ^[14], which gives rise to the [central nervous system](#) ^[15]. During [neurulation](#) ^[13], [ectoderm](#) ^[10] also forms a type of tissue called the [neural crest](#) ^[16], which helps to form structures of the face and brain. The [endoderm](#) ^[9] produced during [gastrulation](#) ^[7] will form the lining of the digestive tract, as well as that of the lungs and thyroid. For animals with three [germ layers](#) ^[6], after the [endoderm](#) ^[9] and [ectoderm](#) ^[10] have formed, interactions between the two [germ layers](#) ^[6] induce the development of [mesoderm](#) ^[12]. The [mesoderm](#) ^[12] forms skeletal muscle, bone, connective tissue, the heart, and the urogenital system. Due to the [evolution](#) ^[17] of the [mesoderm](#) ^[12], triploblastic animals develop visceral organs such as stomachs and intestines, rather than retaining the open digestive cavity characteristic of diploblastic animals.

Christian Pander, a doctoral student of Ignaz Döllinger at the [University of Würzburg](#) ^[18], in Würzburg, Germany, first recognized the existence of [germ layers](#) ^[6] in chicks (*Gallus gallus* ^[19]) in 1817. In the publications derived from his dissertation, Pander described how two layers of cells, which he called serous and mucous, gave rise to an intermediate layer, which he called vascular. Pander wrote of the interdependence of these three layers as well as the necessity of their interaction to form organs.

In 1825, eight years after Pander's initial descriptions, Martin Rathke, a physician and embryologist from Prussia (now Poland), discovered layers of cells in a developing invertebrate [crayfish](#) ^[20], *Astacus astacus* ^[21], that corresponded to those Pander had described in chicks. Rathke showed that the embryonic layers Pander described existed in animals outside of the vertebrate clade. [Karl Ernst von Baer](#) ^[22], a professor of anatomy at the University of Königsberg, in Königsberg, Germany, applied Pander's germ layer concept to all vertebrates in his 1828 *Über Entwicklungsgeschichte der Thiere. Beobachtung und Reflexion* (*On the Developmental History of the Animals. Observations and Reflections*).

Discussion of the [germ layers](#) ^[6] dwindled over the next twenty one years, but they resurfaced when [Thomas Henry Huxley](#) ^[23], a natural historian in England, published "On the Anatomy and Affinities of the Family of the Medusae." In that 1849 text, Huxley suggested that adult jellyfish (Medusae) possessed two tissue layers, which he called foundation membranes, that relate to each other in the same manner that Pander had observed of the serous and mucous layers in the [chick](#) ^[24] embryo. Huxley realized that a correlation existed between the body architecture of the adult jellyfish and the vertebrate embryo. Based on that association, Huxley attempted to integrate the study of vertebrates with that of invertebrates, and to unite studies of development, or [ontogeny](#) ^[25], with studies of organismal relationships, or [phylogeny](#) ^[26]. The relationship between [ontogeny](#) ^[25] and [phylogeny](#) ^[26], later called recapitulation, would be adopted and expanded by proponents of [evolution](#) ^[17], including [Charles Darwin](#) ^[27], in England, and [Ernst Haeckel](#) ^[28], a professor of comparative anatomy at the [University of Jena](#) ^[29], in Jena, Germany.

In the six years following Huxley's publication on Medusae, embryologist [Robert Remak](#) ^[30], in Germany, refined germ layer theory in two ways in his treatise *Untersuchungen über die Bildung und Entwicklung der Wirbelthiere* (*Studies on the Formation and Development of Vertebrates* ^[31]). First, while working as a microscopist, Remak noticed that all of the germ layer cells of the [chick](#) ^[24] embryo derived from the original single cell of the [fertilized egg](#) ^[32]. Thus, Remak concluded, all cells originate from division of pre-existing cells, a conclusion that became central to cell theory. Second, Remak provided histological evidence for the existence of three distinct [germ layers](#) ^[6] and traced the derivatives of each throughout [chick](#) ^[24] development. Few noticed Remak's contributions to cell theory and research on [germ layers](#) ^[6].

In 1867 Aleksandr Kovalevsky, professor of [embryology](#) ^[33] at the University of St. Petersburg, in St. Petersburg, Russia,

published a series of studies that showed the presence of [germ layers](#)^[6] among invertebrates. Kovalevsky's work established the universality and homologous nature of the [germ layers](#)^[6] within the animal kingdom.

According to Jane Oppenheimer, a biologist and historian of science who worked at [Bryn Mawr College](#)^[34] in Philadelphia, Pennsylvania during the twentieth century, Kovalevsky's research prompted some of the most prominent scientists of the nineteenth century to research on the [germ layers](#)^[6]. The concept of the [germ layers](#)^[6] as invariant across species soon became entrenched and formed the basis of germ layer theory. Germ layer theory held that each of the [germ layers](#)^[6], regardless of species, gave rise to a fixed set of organs. In 1872 [Ernst Haeckel](#)^[28] combined observations of [germ layers](#)^[6] with evolutionary theory to hypothesize that an unknown two-layered organism, which he called a [gastraea](#)^[35], was ancestral to all other animals; this came to be known as the Gastraea Theory. One year later, [Edwin Ray Lankester](#)^[36], Professor of Zoology at [University College](#)^[37], London, in London, England, published a theory similar to Haeckel's along with a classification of all animals based on their composition of [germ layers](#)^[6]: homoblastic, diploblastic, and triploblastic. Researchers still use Lankester's classification.

In the late 1870s, several years after Haeckel's and Lankester's publications, many embryologists challenged germ layer theory and Haeckel's Gastraea theory. [Wilhelm His](#)^[38], Rudolf [Albert von Kölliker](#)^[39], and Oscar and Richard Hertwig, all in Germany at the time, objected to the germ layer theory. In a series of publications from 1878 through 1881, the Hertwig brothers provided evidence that the [germ layers](#)^[6] had greater capacities for [differentiation](#)^[40] than most scientists recognized. In 1881 the Hertwigs formulated their Coelom theory, which focused on the role of [mesoderm](#)^[12] and also introduced the term and concept of [mesenchyme](#)^[41], a type of animal tissue derived mostly from [mesoderm](#)^[12].

Amid the varied arguments supporting or denying germ layer theory, some embryologists in the 1890s began to refocus their efforts on methods that could help them further understand how animals develop, and they employed physical manipulations of embryos rather than purely observational or descriptive [embryology](#)^[33]. In 1901 Charles Sedgwick Minot, a professor at [Harvard Medical School](#)^[42] in Boston, Massachusetts, predicted that the transplantation of cells from one germ layer onto another resulted in those cells adopting the fate of their new environment.

More than twenty years later, in 1924, Hilde Proescholdt Mangold and her doctoral advisor at the Zoological Institute in Freiburg, Germany, [Hans Spemann](#)^[43], found evidence for Minot's prediction and dismantled the foundation of the germ layer theory. Mangold harvested presumptive [ectoderm](#)^[10] from the dorsal lip, a tissue that organizes the [gastrula](#)^[44] stage, of an embryonic newt and transplanted this tissue to a different germ layer of the [gastrula](#)^[44] of a second species of newt. The transplanted [ectoderm](#)^[10] responded to the local environment on the developing host newt, and induced the formation of an extra head, nervous system structure, or extra body. That experiment demonstrated that the fates of germ layer cells are not entirely predetermined at the start of development.

In the fifteen years following Mangold's work, embryologists continued to explore the potential for the three [germ layers](#)^[6] to differentiate along different routes and they produced evidence that further weakened the germ layer theory. Sven Hörstadius, professor at Uppsala University, in Uppsala, Sweden, used echinoderms, such as sea urchins, to study how [germ layers](#)^[6] differentiate. He employed transplantation, recombination, and [fate mapping](#)^[45] experiments to investigate the capacity of the [germ layers](#)^[6] to transform into tissues atypical of normal [differentiation](#)^[40].

Throughout the remainder of the twentieth century, researchers continued to accumulate evidence that invalidated the theory that [germ layers](#)^[6] are pre-defined or highly-fated tissues. Following the works of Spemann, Mangold, and Hörstadius, scientists further explored germ layer potential for varied development. In the early 1950s Robert Briggs, at [Indiana University](#)^[46] in Bloomington, Indiana, and Thomas King, at the [Institute for Cancer Research](#)^[47] in Philadelphia, Pennsylvania, transplanted nuclei from the presumptive [endoderm](#)^[9] of the northern leopard [frog](#)^[48], [Rana pipiens](#)^[49], into eggs from which they had removed the nuclei. Briggs and King tracked the development of these transplanted nuclei to explore the timing of cell [differentiation](#)^[40], and with those experiments they laid the foundation for future research in [cloning](#)^[50]. In the late 1960s Pieter D. Nieuwkoop, at the Hubrecht Laboratory in the Royal Netherlands Academy of Arts and Science, in Utrecht, Holland, discovered that [endoderm](#)^[9] induces adjacent [ectoderm](#)^[10] to form [mesoderm](#)^[12]. In the 1980s scientists shifted their focus towards identifying the [genes](#)^[51] that induce structural [differentiation](#)^[40] of the [germ layers](#)^[6]. Researchers in the early twenty-first century investigated the regulatory networks through which individual [genes](#)^[51] interact to cause germ layer [differentiation](#)^[40].

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A germ layer is a group of cells in an embryo that interact with each other as the embryo develops and contribute to the formation of all organs and tissues. All animals, except perhaps sponges, form two or three germ layers. The germ layers develop early in embryonic life, through the process of gastrulation. During gastrulation, a hollow cluster of cells called a blastula reorganizes into two primary germ layers: an inner layer, called endoderm, and an outer layer, called ectoderm. Diploblastic organisms have only the two primary germ layers; these organisms characteristically have multiple symmetrical body axes (radial symmetry), as is true of jellyfish, sea anemones, and the rest of the phylum Cnidaria. All other animals are triploblastic, as endoderm and ectoderm interact to produce a third germ layer, called mesoderm. Together, the three germ layers will give rise to every organ in the body, from skin and hair to the digestive tract.

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[Gastrulation](#) ^[68] [Embryology](#) ^[69] [Cell differentiation](#) ^[70] [Embryos](#) ^[71] [Cells](#) ^[72] [Tissues](#) ^[73] [Anatomy](#) ^[74] [Vertebrates](#) ^[75] [invertebrates](#) ^[76] [Embryological development](#) ^[77] [Organs](#) ^[78] [Organs \(Anatomy\)](#) ^[79] [Blastula](#) ^[80] [Central nervous system](#) ^[81] [Pander, Christian Heinrich, 1794-1865](#) ^[82] [Rathke, Heinrich, 1793-1860](#) ^[83] [Baer, Karl Ernst von, 1792-1876](#) ^[84] [Huxley, Thomas Henry, 1825-1895](#) ^[85] [Lankester, E. Ray \(Edwin Ray\), Sir, 1847-1929](#) ^[86] [Haeckel, Ernst, 1834-1919](#) ^[87] [His, Wilhelm, 1831-1904](#) ^[88] [Spemann, Hans, 1869-1941](#) ^[89] [Nieuwkoop, Pieter D. \(Pieter Dirk\)](#) ^[90] [Germ Layers](#) ^[91]

Topic

[Theories](#) ^[92] [Processes](#) ^[93]

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- [1] <https://embryo.asu.edu/pages/germ-layers>
- [2] <https://embryo.asu.edu/keywords/germ-layer-theory>
- [3] <https://embryo.asu.edu/keywords/mesoderm>
- [4] <https://embryo.asu.edu/keywords/endoderm>
- [5] <https://embryo.asu.edu/keywords/ectoderm>
- [6] <https://embryo.asu.edu/search?text=germ%20layers>
- [7] <https://embryo.asu.edu/search?text=gastrulation>
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- [9] <https://embryo.asu.edu/search?text=endoderm>
- [10] <https://embryo.asu.edu/search?text=ectoderm>
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- [15] <https://embryo.asu.edu/search?text=central%20nervous%20system>
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[72] <https://embryo.asu.edu/library-congress-subject-headings/cells>
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[77] <https://embryo.asu.edu/library-congress-subject-headings/embryological-development>
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