

# Ectoderm <sup>[1]</sup>

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Ectoderm is one of three germ layers—groups of cells that coalesce early during the embryonic life of all animals except maybe sponges, and from which organs and tissues form. As an embryo develops, a single fertilized cell progresses through multiple rounds of cell division. Eventually, the clump of cells goes through a stage called [gastrulation](#) <sup>[2]</sup>, during which the embryo reorganizes itself into the three [germ layers](#) <sup>[3]</sup>: [endoderm](#) <sup>[4]</sup>, [ectoderm](#) <sup>[5]</sup>, and [mesoderm](#) <sup>[6]</sup>. After [gastrulation](#) <sup>[2]</sup>, the embryo goes through a process called [neurulation](#) <sup>[7]</sup>, which starts the development of nervous system.

During [neurulation](#) <sup>[7]</sup>, [ectoderm](#) <sup>[5]</sup> differentiates into two parts. The first is the surface [ectoderm](#) <sup>[5]</sup>, which gives rise to tissues on the outer surface of the body like epidermis, hair, and nails. The second is the neuroectoderm, which forms the nervous system of the embryo. The neuroectoderm further divides into the [neural tube](#) <sup>[8]</sup>, which acts as the precursor for the embryo's [central nervous system](#) <sup>[9]</sup>, and into the [neural crest](#) <sup>[10]</sup>, a collection of mobile cells shed from the junction between the [neural tube](#) <sup>[8]</sup> and the epidermis after the [neural tube](#) <sup>[8]</sup> forms. The [neural crest](#) <sup>[10]</sup> helps form many of the bones and connective tissues of the head and face, as well as parts of the peripheral nervous system. In fishes, the [neural crest](#) <sup>[10]</sup> helps form dorsal fins, and in [turtles](#) <sup>[11]</sup> it helps form the [carapace](#) <sup>[12]</sup>.

The discovery of [ectoderm](#) <sup>[5]</sup> tied to the discoveries of the other [germ layers](#) <sup>[3]</sup>. In 1817 Christian Pander, a doctoral student at the [University of Würzburg](#) <sup>[13]</sup>, in Würzburg, Germany, discovered the [germ layers](#) <sup>[3]</sup> in [chick](#) <sup>[14]</sup> embryos, [Gallus gallus](#) <sup>[15]</sup>. Within his dissertation, Pander described how two layers of cells, which he dubbed the serous and mucous layers, give rise to a third layer, which he called the vascular layer. Pander thereby described the process of [gastrulation](#) <sup>[2]</sup> in the [chick](#) <sup>[14]</sup>, and he brought the three layers of the embryo to the attention of the scientific community. In 1825 physician and embryologist Martin Rathke, in Prussia (later Poland), discovered cell layers in the developing [crayfish](#) <sup>[16]</sup>, [Astacus astacus](#) <sup>[17]</sup>, that corresponded to Pander's serous and mucous layers. Rathke's results showed that these two cell layers existed in the embryos of non-vertebrate animals.

Throughout the nineteenth century, many scientists investigated the [germ layers](#) <sup>[3]</sup>. In 1828 [Karl Ernst von Baer](#) <sup>[18]</sup> at the University of Königsberg, in Königsberg, Prussia, applied Pander's concept of [germ layers](#) <sup>[3]</sup> to all of the vertebrates. In England in 1849 [Thomas Henry Huxley](#) <sup>[19]</sup> used [germ layers](#) <sup>[3]</sup> to unite the vertebrate and invertebrate kingdoms. In his article "On the Anatomy and Affinities of the Family of the Medusae," Huxley compared the anatomy of the jellyfish family and recognized that the two tissue layers he saw in the body plan of the adult jellyfish corresponded with, or were homologous to, the layers in the embryo of the [chick](#) <sup>[14]</sup> that Pander had described. Huxley next coupled the anatomy of an adult organism with the anatomy of an embryo, and he proposed a connection between the study of growth and development, called [ontogeny](#) <sup>[20]</sup>, and the study relationships between organisms or taxa, called [phylogeny](#) <sup>[21]</sup>. The association that Huxley drew between [ontogeny](#) <sup>[20]</sup> and [phylogeny](#) <sup>[21]</sup>, later called recapitulation, influenced other nineteenth century scientists like [Charles Darwin](#) <sup>[22]</sup>, in England, and [Ernst Haeckel](#) <sup>[23]</sup>, in Germany.

In 1853 George James Allman, a naturalist at Trinity College, Dublin, in Dublin, Ireland, coined the terms [ectoderm](#) <sup>[5]</sup> and [endoderm](#) <sup>[4]</sup> to replace Pander's concepts of serous and mucous layers, respectively. Eighteen years later, Huxley, who had by then become professor of [natural history](#) <sup>[24]</sup> at the Royal School of Mines, in London, England, introduced the term [mesoderm](#) <sup>[6]</sup> in his *A Manual of Anatomy of Vertebrated Animals*

By the end of the nineteenth century, the concepts of the [germ layers](#) <sup>[3]</sup> had become the foundation for Germ layer theory, which held that each of the [germ layers](#) <sup>[3]</sup>, regardless of species, gave rise to a fixed set of organs. Many biologists deemed the [germ layers](#) <sup>[3]</sup> homologous across the animal kingdom, effectively uniting [ontogeny](#) <sup>[20]</sup> with [phylogeny](#) <sup>[21]</sup>. Germ layer theory became doctrinal in the late 1860s due to scientists like Alexander Kovalevsky at the University of St. Petersburg, in St. Petersburg, Russia, and [Ernst Haeckel](#) <sup>[23]</sup>, in Germany.

Several scientists opposed Germ Layer Theory, including [Edmund Beecher Wilson](#) <sup>[25]</sup>, in the United States, and [Wilhelm His](#) <sup>[26]</sup>, Rudolf [Albert von Kölliker](#) <sup>[27]</sup>, and brothers Oscar and Richard Hertwig, all in Germany. Most argued that the homology of the [germ layers](#) <sup>[3]</sup> across all taxa was impossible because vertebrates and invertebrates do not all have the same organs.

Widely recognized evidence to disprove germ layer theory came in 1922, from Hilde Proescholdt Mangold and her doctoral advisor, [Hans Spemann](#) <sup>[28]</sup>, working at the Zoological Institute in Freiburg, Germany. Mangold transplanted [ectoderm](#) <sup>[5]</sup> harvested from the dorsal lip, the main organizing tissue of the embryo during [gastrulation](#) <sup>[2]</sup>, between donor and host species of newts. The embryos in which she had transplanted the dorsal lip developed an extra body, head, or other nervous system structure. The resultant newts indicated that the transplanted tissue had induced [gastrulation](#) <sup>[2]</sup> and [neurulation](#) <sup>[7]</sup> of surrounding

tissue just as it would have in its parent embryo. Mangold's experiments proved that the [germ layers](#)<sup>[3]</sup> lacked absolutely determined derivatives, a result that dismantled germ layer theory. Additionally, this experiment exemplified a shift in embryological methods that had occurred in the late nineteenth century. Whereas most practitioners had focused on described and compared the anatomy of different embryos, some scientists began to physically manipulate embryos to test hypotheses. These methods helped spur the growth of programs that focused on experimental [embryology](#)<sup>[29]</sup> during the early twentieth century.

Following the work of Mangold and Spemann, other scientists experimented on the three [germ layers](#)<sup>[3]</sup>. Among these experimental embryologists was Sven Hörstadius at Uppsala University, in Uppsala, Sweden. Conducting experiments on [echinoderms](#)<sup>[30]</sup>, a phylum that includes sand dollars and sea urchins, Hörstadius investigated the ability of the [germ layers](#)<sup>[3]</sup> to transform. Among Hörstadius' major contributions was his work on the [neural crest](#)<sup>[10]</sup>, which culminated in a book in 1950 titled *The Neural Crest: Its properties and derivatives in the light of experimental research*

[Wilhelm His](#)<sup>[26]</sup> at the [University of Basel](#)<sup>[31]</sup>, in Basel, Switzerland, had discovered [neural crest](#)<sup>[10]</sup>, a derivative of the neuroectoderm, in the [chick](#)<sup>[14]</sup> in 1868. He noticed that as the [neural tube](#)<sup>[8]</sup> closed, cells began to migrate away from midline; these cells eventually became called the [neural crest](#)<sup>[10]</sup>. Twenty years later scientists had begun to look for the derivatives of the [neural crest](#)<sup>[10]</sup>, especially in the head and nervous system. In 1893 Julia Platt, a doctoral student studying at Munich University, in Munich, Germany, published the results of her research on the ectodermal, specifically [neural crest](#)<sup>[10]</sup>, derivatives in the head. Based on her studies of [Necturus maculosus](#)<sup>[32]</sup> embryos, a type of aquatic [salamander](#)<sup>[33]</sup>, Platt showed that the cartilage of the branchial arches and parts of the teeth developed from [ectoderm](#)<sup>[5]</sup>.

Few scientists acknowledged the role of [neural crest](#)<sup>[10]</sup> in the formation of the skeleton until the 1940s when Hörstadius and Sven Sellman, in Sweden, and Gavin de Beer, in England, confirmed the role of [neural crest](#)<sup>[10]</sup> in skeletal development. During the 1960s, researchers studied how [neural crest cells](#)<sup>[34]</sup> migrate. Researchers like James Weston at [Yale University](#)<sup>[35]</sup>, in New Haven, Connecticut, and Malcolm Johnston, at the University of Rochester, in Rochester, New York, traced the migration of trunk and cranial [neural crest](#)<sup>[10]</sup> in [chick](#)<sup>[14]</sup> embryos. In the 1970s, Nicole Le Douarin, a researcher at the University of Nantes, in Nantes, France, created chimeric quail and [chick](#)<sup>[14]</sup> embryos to track the migration and derivatives of the [neural crest](#)<sup>[10]</sup>.

As some researchers investigated the derivatives and movements of [neural crest](#)<sup>[10]</sup>, others examined the interactions of the different [germ layers](#)<sup>[3]</sup> within the embryo. In 1969 Pieter D. Nieuwkoop, at the Royal Netherlands Academy of Arts and Science, in Utrecht, Holland, published an article that addressed the potential of [endoderm](#)<sup>[4]</sup> and [ectoderm](#)<sup>[5]</sup> to induce the formation of their surrounding tissues. Using embryos of the [salamander](#)<sup>[33]</sup> [Ambystoma mexicanum](#)<sup>[36]</sup>, Nieuwkoop showed that when [endoderm](#)<sup>[4]</sup> and [ectoderm](#)<sup>[5]</sup> interact, the [endoderm](#)<sup>[4]</sup> induces [mesoderm](#)<sup>[6]</sup> to form within the adjacent regions of [ectoderm](#)<sup>[5]</sup>. His experiments also demonstrated that the establishment of the ventral and dorsal regions of the embryo, known as the [polarity](#)<sup>[37]</sup> of the embryo, results from the interactions of the [endoderm](#)<sup>[4]</sup> and [ectoderm](#)<sup>[5]</sup>.

Scientists began to research the genetic signals responsible for [gastrulation](#)<sup>[2]</sup> in the mid-1980s. Families of signaling factors, such as Vg1/Nodal, Wnt, and FGF, produce proteins that help to pattern the embryo and to form the three [germ layers](#)<sup>[3]</sup>. In the 1990s, scientists began to show how the signals involved in [gastrulation](#)<sup>[2]</sup> also function in [neurulation](#)<sup>[7]</sup>. In particular, researchers studied the Bone Morphogenetic Protein, or BMP, pathway. This pathway of signals helps cause tissues to differentiate during [gastrulation](#)<sup>[2]</sup>, with inhibition of BMP causing the [ectoderm](#)<sup>[5]</sup> to differentiate into neuroectoderm, the tissue that gives rise to the nervous system. Researchers found that proteins like Chordin, Noggin, Follistatin, and Cerberus block the expression of different members of the BMP family. These BMP-inhibitors help to induce the [ectoderm](#)<sup>[5]</sup> to differentiate into the central and peripheral nervous systems.

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Ectoderm is one of three germ layers--groups of cells that coalesce early during the embryonic life of all animals except maybe sponges, and from which organs and tissues form. As an embryo develops, a single fertilized cell progresses through multiple rounds of cell division. Eventually, the clump of cells goes through a stage called gastrulation, during which the embryo reorganizes itself into the three germ layers: endoderm, ectoderm, and mesoderm. After gastrulation, the embryo goes through a process called neurulation, which starts the development of nervous system.

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