Julia Barlow Platt's Embryological Observations on Salamanders' Cartilage (1893) [1]

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In 1893, Julia Barlow Platt published her research on the origins of cartilage in the developing head of the common mudpuppy (*Necturus maculosus* [3]) embryo. The mudpuppy is an aquatic salamander [4] commonly used by embryologists because its large embryonic cells and nuclei are easy to see. Platt followed the paths of cells in developing mudpuppy embryos to see how embryonic cells migrated during the formation of the head. With her research, Platt challenged then current theories about germ layers, the types of cells in an early embryo that develop into adult cells. In most organisms’ development, three types of germ layers are responsible for the formation of tissues and organs. The outermost layer is called *ectoderm* [5], the middle layer *mesoderm* [6], and the innermost layer *endoderm* [7], although Platt called it entoderm. Platt's research provided a basis for scientists to clarify the destination or function of the germ layers [8] in vertebrates' development.

Platt started her research on *Necturus* at the University of Chicago in Chicago, Illinois, under the guidance of her mentor and chairman of the zoology department, Charles Otis Whitman [9]. She later continued that work at the Ludwig Maximilian University of Munich in Munich, Germany. In 1893, Platt published a journal article in which she demonstrated that cartilage and the skeletal tissue that forms teeth in the head of a mudpuppy embryo develop from the ectodermic or most exterior germ layer of cells. Platt's research contradicted the hypothesis held at the time, called the germ layer theory, which stated that connective tissues such as bone, muscle, and cartilage, originated from the mesodermic or middle layer and that tissues of similar function always originated from the same corresponding germ layer.

The three main germ layers [8] of an early animal embryo are *ectoderm* [5], *mesoderm* [6], and *endoderm* [7]. Upon fertilization [10], an embryo of an egg [11]-laying animal starts to divide and form an early hollow body called a blastula [12], which then folds in on itself (invaginates) to form a gastrula [13]. Inside the gastrula [13] three layers of cells form, and they are the main contributors to what will become the cells and tissues of the adult.

In the nineteenth century Christian Pander, a graduate student in University of Würzburg [14] in Würzburg, Germany, introduced the germ layer theory when he described the different developmental layers of cells that corresponded to different parts of the body in a developing chick [15] embryo. In 1828, the scientific community accepted the germ layer theory when Karl Ernst von Baer [16] at the University of Dorpat [17] in Dorpat, later called Tartu, Estonia, hypothesized that each layer developed into specific tissues, and that the same kinds of tissues developed from the same kinds of germ layers [9] in all vertebrates. Later in 1867, Aleksandr Kovalevsky at the University of St. Petersburg in St. Petersburg, Russia, supported and extended the germ layer theory with his studies on invertebrates.

Some of Platt's contemporaries, including Albert Oppel [18] at the University of Munich [19] in
Munich, Germany, and other scientists started to question the germ layer theory and published separate studies of ectodermic cell proliferation in cartilaginous fish (Elasmobranchii) [20], chick (Gallus gallus) [22], and slow worm legless lizards (Anguis fragilis) [23]. Their results indicated that ectoderm [5] contributed part of the developing tissue of mesenchymal cells, which originate mostly from mesoderm [6] and develop into connective tissue and the circulatory and lymphatic systems. The results of their research were not obvious since only part and not the whole tissue was derived from ectoderm [5] and the rest was derived from mesoderm [6].

In the early 1890s, Platt developed her hypothesis that the head cartilage of mudpuppies originated from the ectoderm [5]. Before Platt published her research, N. Kastschenko at the University of Kharkiv in Kharkiv, Ukraine, had observed that in Elasmobranchs, ectoderm [5] contributed to mesenchyme [24] production in the nose, mouth, and branchial clefts. Nikolaus Goronwitsch had proposed something similar for chick [15] embryos. Oppel had observed that ectoderm [5] proliferated into the mesoderm [6] layer, and Platt later observed the same phenomenon. Platt later investigated the development of the head in mudpuppies in a way that questioned the germ layer theory, which the scientific community had accepted.

Platt's research of mudpuppies consisted of observing the mudpuppy embryos during their development. In some cases, Platt observed them with unaided sight, while in other cases she used microscopes. Platt observed that in the developing embryo, endodermic cells surrounded the yolk [25] sac, the part of the egg [11] that transfers yolk [25] granules or yolk [25] platelets to the rest of the embryo to provide nutrients. Platt used the different size and quantity of yolk [25] granules in ectodermic and mesodermic cell layers as a marker to identify those types of cells, and to observe their movement during development. She found that the head cartilage originated from the ectoderm [5] layer, which meant that the three germ layers [8] are not always exclusive to a certain type of differentiated cell. With her research, Platt questioned the germ layer theory, which stated that ectoderm [5] only produced skin and brain structures, while all vascular, bone, muscle, and connective tissues like cartilage were expected to develop from mesoderm [6].

Platt published her results in the journal article titled "Ectodermic Origins of the Cartilages of the Head" in 1893. Initially, some scientists did not accept Platt's research because her results did not corroborate the already established assumptions of the germ layer theory, which stated that cartilage derived from the mesoderm [6] layer. Platt's results started a controversy among her peers in the developmental biology community, with both sides publishing statements either denying or supporting her findings. One of her critics, Charles Sedgwick Minot, the president of the American Association for the Advancement of Science in the US, rejected Platt's results on the grounds that he had compared the developmental stages [26] of the frog [27] Rana temporaria [28] and did not find any evidence of the processes Platt had observed in mudpuppies. Felix Anton Dohrn [29], director of the Stazione Zoologica [30] in Naples, Italy, agreed with and defended Platt's results after examining his own data on shark [31] embryos. The discussion Platt started encouraged scientists to look closer at the germ layer theory and how it related to the developing embryos of different species.

After Platt published her paper, Leon S. Stone at Yale University [32] in New Haven, Connecticut, Sven Hörstadius at Uppsala University in Uppsala, Sweden, and Drew Noden at Cornell University in Ithaca, New York, conducted multiple experiments that corroborated Platt's results.


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