Gastrulation in Xenopus [1]

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The process of gastrulation [6] allows for the formation of the germ layers [7] in metazoan embryos, and is generally achieved through a series of complex and coordinated cellular movements. The process of gastrulation [6] can be either diploblastic or triploblastic. In diploblastic organisms like cnidaria or ctenophora, only the endoderm [8] and the ectoderm [9] form; in triploblastic organisms (most other complex metazoans), triploblastic gastrulation [6] produces all three germ layers [7]. The gastrula [10], the product of gastrulation [6], was named by Ernst Haeckel [11] in the mid-1870s; the name comes from Latin, where gastēr means stomach, and indeed the gut (archenteron) is one of the most distinctive features of the gastrula [10].

Since the early twentieth century, experimental embryologists like Hans Spemann [12] and Wilhelm Roux [13] have extensively studied gastrulation [6] in amphibian embryos in an attempt to learn more about how establishment of different regions in the body is determined. The size and structure of *Xenopus laevis* [14] (African clawed frogs) embryos have made the species into a model organism [15] for early developmental study. The following is a detailed explanation of gastrulation [6] in *Xenopus*; while gastrulation [6] varies across species, studies in *Xenopus* have shed considerable light on the process in general.

The raw material for gastrulation [6] is the blastula [16], a hollow sphere of cells; the space inside of the blastula [16] is called the blastocoel [17]. If the blastula [16] were compared to a globe of the world, the North Pole would correspond to the animal pole of the embryo, and the South Pole to the embryo's vegetal pole. The hemispheres of the blastula [16] correspond to the names of their respective poles. Cellular division occurs much more rapidly near the animal (active) pole of the frog [18] embryo than near the yolkier vegetal (sedentary) pole; the yolk [19] provides the embryo with nutrition, but slows down cell division around it. The equator between the two hemispheres is called the marginal zone. The blastocoel [17] occupies most of the inside of the animal hemisphere, since the cells in the vegetal pole bear the yolk [19] of the embryo and therefore occupy more of the inner space in that region.

While the animal-vegetal gradient is determined in the egg [20] prior to fertilization [21], the point of entry of the sperm [22] lends the frog [18] its dorsal-ventral (back-and-front) axis. The prospective ventral side of the embryo is on the side of the sperm's entry, while the prospective dorsal side, the side at which the blastopore [23] forms, is opposite the sperm's point of entry. The blastopore [23] is a groove in the side of the embryo that results from the invagination (the formation of a groove) of a small group of future endodermal cells, and forms right below the equator of the embryo, in the marginal zone. Here, cells undergo apical constriction to become “bottle” cells (tapered cells resembling narrow Erlenmeyer flasks); since most of the cytoplasm in each of these cells is made to migrate toward the center of the embryo, the part of the cell in contact with the groove to become much narrower. The lip of the blastopore [23] nearer to the animal pole is termed the dorsal lip of the blastopore [23].

Once the blastopore [23] has formed, the cells of the animal hemisphere undergo epiboly (flattening of the outer layer of cells and radial intercalation of the layer of cells beneath them) and move toward the blastopore [23]. As these cells divide and extend to envelope the inside of the developing frog [18], the marginal zone cells involute (or fold inward) at the dorsal lip of the blastopore [23]. During involution, these inner cells move toward the dorsal lip and then fold over themselves and progress toward the animal pole (the top of the embryo). While the location at which the involuting cells change direction remains the dorsal lip of the blastopore [23], the cells passing through that point change: as the original tapered bottle cells involute, they are replaced by precursor cells for the head mesoderm [24], followed by chordamesoderm cells. The latter will go on to form the notochord [25] of the embryo. It is important to note that this involution depends on the movement of the deep marginal zone cells, as opposed to the movement of the superficial bottle cells of the blastopore [23].

While cells are involuting and the pre-ectoderm [9] is going through epiboly, the blastocoel [17] moves ventrally (up and away from the dorsal lip of the blastopore [23], and then eventually around toward the vegetal pole) and shrinks as the involuting cells progressively move in to occupy the region, much like how frost creeps up a window on a cold day. The involuting marginal zone cells progress ventrally to line the roof of the archenteron (the gut) which expands in proportion to the disappearance of the blastocoel [17]. As it forms, the archenteron itself resembles a balloon that is being inflated through the blastopore [23] and into the animal hemisphere.

When epiboly and involution near completion, the material of the vegetal hemisphere closest to the blastopore [23] becomes constricted by the dorsal and ventral blastopore [23] lips to form a circular yolk [19] plug. This yolk [19] plug then continues to shrink as ectodermal epiboly progresses, and is eventually absorbed into the embryo; the inner layer, formed from vegetal pole cells, becomes the endoderm [8]. The mesoderm [24] constitutes the region between the superficial ectoderm [9] and the internal endoderm [8], and lines the upper part of the archenteron. At the end of gastrulation [6], the *Xenopus* embryo becomes known as a gastrula [10]. It has an ectoderm [9] as its outermost layer, and an endoderm [8] as its innermost layer. The mesoderm [24] lies between the two layers, and the endoderm [8] and mesoderm [24] line the archenteron of thegastrula [10].

While *Xenopus* serves as the model organism [15] for study of amphibian gastrulation [6], some key differences exist in the process across the class. The amphibian class is made up of three major orders: anura (tailless amphibians [26] like frogs), caudata/ urodela (tailed amphibians [26] like salamanders) and caecilians (legless amphibians [26], snake [27]-like). Whereas in *Xenopus* the pre-mesodermal tissues originate exclusively from the deeper marginal zone, urodeles derive mesodermal tissue from both superficial and deeper marginal zone cells. In addition, in the 1940s German embryologist Johannes Holtfreter [28] was able to show that the dorsal marginal zone cells, i.e., the bottle cells of the blastopore [23], serve a crucial role in involution and can even induce a blastopore [23] to form in urodeles. This is not the case with*Xenopus*, which indeed relies on the bottle cells for initiation, but not for the continuance of the gastrulation [6].

Gastrulation is crucial to the proper development of all multicellular animals, especially those with complex tissue structure. Designation of the ectoderm [9] is essential for the later formation of the epidermis (skin) and nervous system. Themesoderm [24] gives rise to the skeleton, muscles, connective tissue, blood and internal organs. The endoderm [8], the innermost germ layer, goes on to form other organs like the lungs, liver, and pancreas as well as the lining of the digestive tract.

Studies of gastrulation [6] in *Xenopus* have allowed developmental biologists to construct accuratefate maps [29] and to make inferences regarding the ontogeny [30] of amphibians [26]. Amphibians have therefore provided the means for a better understanding of the process by which a mass of relatively undifferentiated cells transforms into an intricate and functional organism. While *Xenopus,* in particular, entered the field ofembryology [31] as an already-established clinical tool for effective pregnancy [32] assays, this frog [18] species soon became a prominent model organism [15] for experimental embryologists, and continues to aid greatly in the investigation of ontogeny [30].

Sources

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Subject

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