



Review

Gastrulation and pre-gastrulation morphogenesis, inductions, and gene expression: Similarities and dissimilarities between urodelean and anuran embryos

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ABSTRACT

Studies of meso-endoderm and neural induction and subsequent body plan formation have been analyzed using mainly amphibians as the experimental model. *Xenopus* is currently the predominant model, because it best enables molecular analysis of these induction processes. However, much of the embryological information on these inductions (e.g., those of the Spemann–Mangold organizer), and on the morphogenetic movements of inductively interacting tissues, derives from research on non-model amphibians, especially urodeles. Although the final body pattern is strongly conserved in vertebrates, and although many of the same developmental genes are expressed, it has become evident that there are individually diverse modes of morphogenesis and timing of developmental events. Whether or not this diversity represents essential differences in the early induction processes remains unclear. The aim of this review is to compare the gastrulation process, induction processes, and gene expressions between a urodele, mainly *Cynops pyrrhogaster*, and an anura, *Xenopus laevis*, thereby to clarify conserved and diversified aspects. *Cynops* gastrulation differs significantly from that of *Xenopus* in that specification of the regions of the *Xenopus* dorsal marginal zone (DMZ) are specified before the onset of gastrulation, as marked by blastopore formation, whereas the equivalent state of specification does not occur in *Cynops* until the middle of gastrulation. Detailed comparison of the germ layer structure and morphogenetic movements during the pre-gastrula and gastrula stages shows that the entire gastrulation process should be divided into two phases of notochord induction and neural induction. *Cynops* undergoes these processes sequentially after the onset of gastrulation, whereas *Xenopus* undergoes notochord induction during a series of pre-gastrulation movements, and its traditionally defined period of gastrulation only includes the neural induction phase. Comparing the structure, fate, function and state of commitment of each domain of the DMZ of *Xenopus* and *Cynops* has revealed that the true form of the Spemann–Mangold organizer is suprablastoporal *gsc*-expressing endoderm that has notochord-inducing activity. *Gsc*-expressing deep endoderm and/or superficial endoderm in *Xenopus* is involved in inducing notochord during pre-gastrulation morphogenesis, rather than both *gsc*- and *bra*-expressing tissues being induced at the same time.

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Introduction

Gastrulation is a set of evolutionarily conserved morphogenetic movements in the early development of a wide variety of vertebrates. During gastrulation in amphibians, the cells of the dorsal marginal zone (DMZ) involute through the blastopore to form an archenteron roof (ARF) that underlies the future central

nervous system (CNS). The three-dimensional germ layer structure of the embryo is established during gastrulation, and two major inductive interactions are required. One is meso-endoderm induction and establishment of the anteroposterior and dorsoventral regional characteristics of the induced mesoderm. The other is neural induction, in which induced and regionally specific mesoderm within the ARF or associated with it, spatially and temporally interacts with the presumptive neuroectoderm to form the CNS. Thus, the early patterning of the embryo involves a complex set of spatial and temporal inductions, morphogenetic movements and regional interactions.

Spemann and Mangold (1924) first discovered in urodeles the organizational activity of the early gastrula dorsal blastoporal lip

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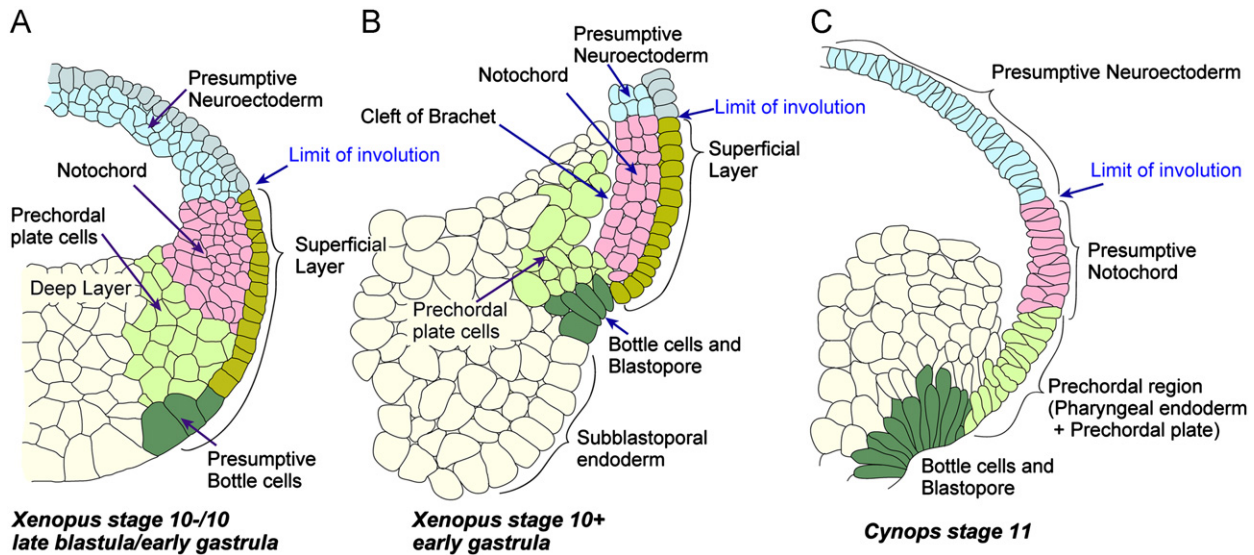


Fig. 1. Structure of the dorsal marginal zone (DMZ) of *Xenopus* and *Cynops* early gastrulae. The *Xenopus* early gastrula DMZ has superficial and deep layers. At the late blastula/early gastrula stage (A), the superficial layer is subdivided into prospective archenteron roof (ARF) endoderm, part of the prospective dorsal mesoderm and prospective bottle cells. The deep layer has sub-classes of leading edge meso-endoderm (LEM) of the future pharyngeal endoderm/prechordal plate and notochord. At stage 10+ when bottle cells are formed (B), the deep layer has already started to involute, independent of bottle cell formation, by pre-gastrulation morphogenesis and the Cleft of Brachet is formed. At this stage, the involuting LEM starts to vertically contact the surface neuroectoderm (Modified from Bauer et al., 1994; Harland and Gerhart, 1997; Arendt and Nübler-Jung, 1999; Shook et al., 2004 and Keller and Shook, 2004). (C) At the early gastrula stage when bottle cells are formed, the *Cynops* DMZ is defined as the area between the blastopore and the limits of involution. The DMZ is a single-cell-layered structure except at its most vegetal (future anterior) part, and is divided into a vegetal (future anterior) prechordal region and an animal (future posterior) presumptive notochord, arranged in a planar juxtaposition. (Modified from Suzuki et al., 1997).

(DLP¹), which can induce an ectopic secondary axis when transplanted into another part of the embryo. These basic concepts of the organizer were then widely investigated by comprehensive embryological experiments using mainly urodele embryos as the model (reviewed by Nieuwkoop et al., 1985; Hamburger, 1988). The heritage of embryological knowledge derived from urodele experimental embryology is translated into the current amphibian model of the anuran, *Xenopus laevis*, which best enables analysis of the molecular nature of the meso-endoderm and neural induction processes. However, there may be some misinterpretation of basic embryological processes, because *Xenopus* and urodeles differ significantly in the structure of their respective DMZ, the state of commitment of the early gastrula DMZ, the mode of morphogenetic movement and the spatiotemporal interactions between the ARF and the overlying presumptive neuroectoderm (for reviews, see Nieuwkoop, 1996, 1997).

Comparative studies of gastrulation mechanisms (Shook and Keller, 2008a, b), developmental profiles (Ninomiya et al., 2001; Collazo and Keller, 2010) and gene expression patterns (Beckham et al., 2003; del Pino et al., 2007; Moya et al., 2007; Nath and Elinson, 2007; Venegas-Ferrín et al., 2010) of several members of the Urodele and Anura families have been performed and the results compared with those for *Xenopus*. From these it has become evident that the gastrulation mechanism and/or the timing of gene expression in the embryo differs according to the embryo's size, developmental speed and/or amount and omnipresence of yolk (for reviews, see Arendt and Nübler-Jung, 1999; Elinson and Beckham, 2002; Solnica-Krezel, 2005; Callery, 2006). For example, in frogs with slow development, the mesoderm may become specified later than in *Xenopus* (del Pino et al., 2007; Moya et al., 2007). Recently, the gene regulatory network (GRN)

for endoderm and mesoderm specification and differentiation, and its essential role in body plan formation, have been elucidated (e.g., Swiers et al., 2010; Rankin et al., 2011; for review, see Davidson and Erwin, 2006). These results suggest that there are generally conserved but individually diverse modes of morphogenesis even among the anuran species. However, whether or not this diversity represents essential differences in the early patterning of the embryo remains obscure. Although the final antero-posterior and dorsoventral body patterns and maps of gene expression domains are strongly conserved in all vertebrates (Elinson and Kezmoh, 2010), it is necessary to analyze the similarities and dissimilarities of these basic processes to deepen our understanding of the fundamental principles of the early patterning of the embryos. In this review, we aim to verify the similarities and dissimilarities of the gastrulation process, and the spatially and temporally controlled mesoderm and neural induction processes, mainly from an embryological point of view, between a urodele, primarily the Japanese newt *Cynops pyrrhogaster* (formerly *Triturus pyrrhogaster*) and an anura, *Xenopus laevis*, both of which have extensive data and histories of investigation.

Structure, prospective fate, morphogenesis and functional gene expression domains of the urodele and anuran early gastrula DMZ

The spatial location or topological architecture of the DMZ varies among vertebrates but the essential feature is well conserved (Arendt and Nübler-Jung, 1999; Solnica-Krezel, 2005). In amphibians, the early gastrula DMZ occupies an arc-shaped region restricted to the dorso-vegetal part of the embryo. The DMZ is a mixture of multiple heterologous domains with differing prospective fates, self-differentiation and functions. However, the early gastrula DMZ of both *Xenopus* and *Cynops* shows considerable differences in its germ layer structure (Figs. 1 and 2 and Table 1).

¹ DLP is often used as a synonym for "organizer" or "DMZ". However, in many earlier experiments, the stage criterion, size and location of the DLP were not always defined. Throughout the text we use DLP to mean the upper blastopore generally, at any given stage, and DMZ as the stage- and site-defined upper blastopore region of the beginning gastrula.

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