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Dorsoventral patterning of the *Drosophila* hindgut is determined by interaction of genes under the control of two independent gene regulatory systems, the dorsal and terminal systems

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ABSTRACT

Dorsoventral (DV) patterning in the trunk region of *Drosophila* embryo is established through intricate molecular interactions that regulate Dpp/Scw signaling during the early blastoderm stages. The hindgut of *Drosophila*, which derives from posterior region of the cellular blastoderm, also shows dorsoventral patterning, being subdivided into distinct dorsal and ventral domains. *engrailed* (*en*) is expressed in the dorsal domain, which determines dorsal fate of the hindgut. Here we show that a repressor Brk restricts *en* expression to the dorsal domain of the hindgut. Expression domain of brk during early blastdermal stages is defined through antagonistic interaction with *dpp*, and expression domains of *dpp* and *brk* in the early blastoderm include prospective hindgut domain. After stage 9, *dpp* expression in the dorsal domain of the hindgut primordium disappears, but, the *brk* expression in the ventral domain continues. It was found that *Dorsocross* (*Doc*), which is a targe gene of Dpp, is responsible for restricting *brk* expression to the ventral domain of the hindgut. On the other hand, activation of *en* is under the control of *brachyenteron* (*byn*) that is regulated independently of *dpp*, *brk*, and *Doc*. The cooperative interaction of common DV positional cues with *byn* during hindgut development represents another aspect of mechanisms of DV patterning in the *Drosophila* embryo.

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1. Introduction

Patterning of the *Drosophila* embryo is based on the anteroposterior (AP) and dorsoventral (DV) body axes established by four independent gene regulatory systems: the anterior, posterior, terminal, and dorsal systems (Nüsslein-Volhard, 1991). Activity gradient of the maternal Dorsal protein along the DV axis initially sets up a prepattern of prospective domains of the mesoderm, neuroectoderm, and dorsal ectoderm by regulating subordinate genes (Rusch and Levine, 1996). A BMP-type ligand Decapentaplegic (Dpp) is expressed in dorsal 40% of the early blastoderm, and plays a pivotal role in DV patterning of the trunk ectoderm as a morphogen (Podos and Ferguson, 1999; Raftery and Sutherland, 1999).

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The highest level of Dpp/BMP signal determines the dorsalmost structures, while prospective dorsal and dorsolateral epidermis are determined by lower signal levels (Arora et al., 1994; Ashe et al., 2000; Podos and Ferguson, 1999; Raftery and Sutherland, 2003; Shimmi et al., 2005; Wang and Ferguson, 2005). A transcriptional repressor Brk, which is expressed in ventrolateral region of the early blastoderm, is also essential for the DV patterning. Brk represses target genes of the Dpp signal while transcription of *brk* is repressed by Dpp (Jazwinska et al., 1999a,b; Campbell and Tomlinson, 1999; Minami et al., 1999; Podos and Ferguson, 1999; Sivasankaran et al., 2000; Affolter et al., 2001). In *brk* mutant embryos, dorsal ectoderm expands ventrally at the expense of the neuroectoderm (Affolter et al., 2001; Jazwinska et al., 1999b). Most studies on DV patterning in *Drosophila* have focused on the trunk region, but, some organs that arise outside the trunk also show DV patterning. Development of the embryonic dorsal head region depends on Dpp signal gradient (Chang et al., 2001), suggesting that the common genetic mechanisms of DV patterning are working outside the trunk region.

The hindgut is another example of organs that show distinct DV patterning (Murakami et al., 1994, 1999; Takashima and Murakami, 2001; Murakami and Shiotsuki, 2001; Takashima et al., 2002). The hindgut of *Drosophila* derives from the ectoderm invaginated from posterior region of the blastoderm (Lengyel and Liu, 1998; Murakami et al., 1999; Lengyel and Iwaki, 2002), and its development is regulated by the *Brachyury* ortholog *brachyenteron* (*byn*), which is activated under the control of the terminal system (Kispert et al., 1994; Murakami et al., 1995; Singer et al., 1996). The major middle portion of the hindgut, which is called the large intestine, is subdivided into dorsal and ventral domains that are characterized by distinct cellular morphology and gene expression (Murakami and Shiotsuki, 2001; Takashima and Murakami, 2001). *engrailed* (*en*) is expressed continuously in the dorsal domain of the hindgut (Hama et al., 1990; Takashima and Murakami, 2001), and it acts as a selector gene determining the dorsal fate by repressing ventral fate (Takashima and Murakami, 2001; Iwaki and Lengyel, 2002; Takashima et al., 2002). In this paper, we use only the terms "DV subdivision of the hindgut" instead of "DV subdivision of the large intestine of the hindgut". In addition to the simple tissue organization, cellular composition of the hindgut is also very simple: each domain consists of a single cell type (Murakami et al., 1994; Murakami and Shiotsuki, 2001), which makes the hindgut suitable for analyzing cell differentiation along the DV body axis. It is reasonable to assume that, in addition to positional cues from the terminal system, DV positional cues in the blastoderm

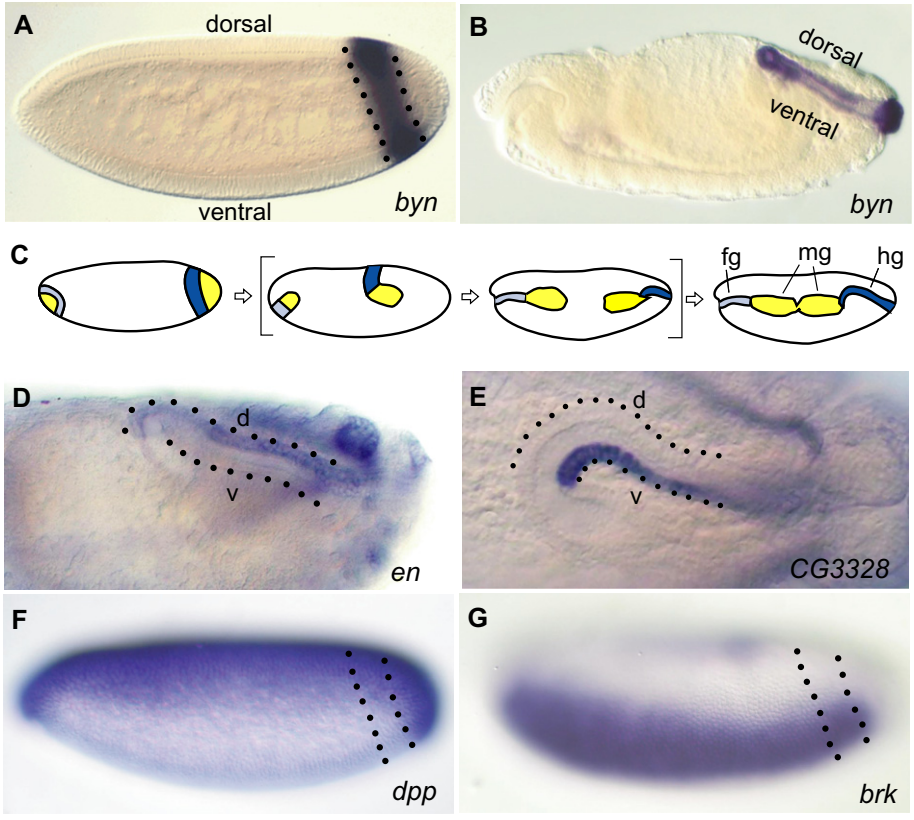

Fig. 1 – DV patterning of the hindgut, with an outline of the hindgut morphogenesis. The dotted lines indicate outline of the prospective or invaginated hindgut. Prospective hindgut region is discernible by the expression of *byn* in the early blastoderm (A). After invagination, the *byn*-positive region forms a hindgut tube (B). (C) Schematic illustrations of morphogenesis of the hindgut: prospective and developing hindgut (hg) are blue; the anterior and posterior endoderms, which form the midgut (mg), are yellow; the prospective foregut (fg) is pale blue. (D and E) After the invagination, the dorsal domain (d) of the hindgut tube expresses *en* (D), and the ventral domain (v) expresses a marker gene, *CG3328* (E). (F and G) The *byn*-positive region in the early blastoderm partially overlaps both *dpp*-positive (F) and *brk*-positive (G) regions.

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