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Review

Heads and tails: Evolution of antero-posterior patterning in insects

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ABSTRACT

In spite of their varied appearances, insects share a common body plan whose layout is established by patterning genes during embryogenesis. We understand in great molecular detail how the *Drosophila* embryo patterns its segments. However, *Drosophila* has a type of embryogenesis that is highly derived and varies extensively as compared to most insects. Therefore, the study of other insects is invaluable for piecing together how the ancestor of all insects established its segmented body plan, and how this process can be plastic during evolution.

In this review, we discuss the evolution of Antero-Posterior (A-P) patterning mechanisms in insects. We first describe two distinct modes of insect development – long and short germ development – and how these two modes of patterning are achieved. We then summarize how A-P patterning occurs in the long-germ *Drosophila*, where most of our knowledge comes from, and in the well-studied short-germ insect, *Tribolium*. Finally, using examples from other insects, we highlight differences in patterns of expression, which suggest foci of evolutionary change.

1. Introduction

In spite of their varied appearances, insects have in common a body plan that consists of head, thorax, and abdomen, with different numbers and types of segments. Insects generally possess a head region made up of 6–7 segments, a thorax of three segments, and an abdomen of 8–11 segments. This format is laid out during embryogenesis when patterning genes specify the body plan. Virtually all insects start development in a syncytial environment where nuclei divide without cell membranes to separate cells. Patterning factors may thus diffuse and have direct access to nuclei to provide patterning information. We currently have a high molecular resolution map in *Drosophila* of how an embryo patterns its segments. However, *Drosophila* has a highly derived type of embryogenesis in which virtually all segments are patterned simultaneously at the syncytial stage. Therefore, the study of other insects is invaluable for piecing together how the ancestor of all insects established its segmented body plan, and how this process can be plastic during evolution. Though we only have extensive molecular understanding of the development of very few non-drosophilid insects, these data show that, while the paths taken to achieve similar adult body plans share common features, they are often very different.

This review will discuss the evolution of Antero-Posterior (A-P) patterning mechanisms in insects. It will first describe the two distinct modes of insect development, long and short germ development, and how these two modes of patterning are achieved. We will then summarize how A-P patterning occurs in the long-germ *Drosophila*, where most of our knowledge comes from, and in the well-studied short-germ insect, *Tribolium*. Examples drawn from other insects will highlight differences in patterns of expression, but also foci of evolutionary change.

1.1. Germ types

G. Krause is credited with the designations now in use to distinguish among the different developmental strategies used by insects ([1]; Fig. 1). He observed that some insects produce eggs in which the antecedents ("anlagen") of all the future segments of the embryo are represented and patterned during the syncytial blastoderm stage. Since the embryo ("germ") fills up the majority of the egg and all segments of the germ anlage are present before gastrulation, with a relatively small portion designated for extra-embryonic tissue, he called these embryos "large germ". These embryos were also called "long germ" referring in part to the number of segments specified in the germ anlage by the time gastrulation occurred ([1,2]; Fig. 1A). Embryos that fall into this category include the higher Diptera *Drosophila melanogaster* and *Musca domestica* [3–5], as well as the parasitic wasp *Nasonia vitripennis* (Hymenoptera) [6]. In contrast, Krause noted that other insects produce eggs in which most of the material is specified as extraembryonic tissue, with the germ tissues largely restricted to the posterior–ventral side of the egg. In these insects, only the anteriormost embryonic structures are

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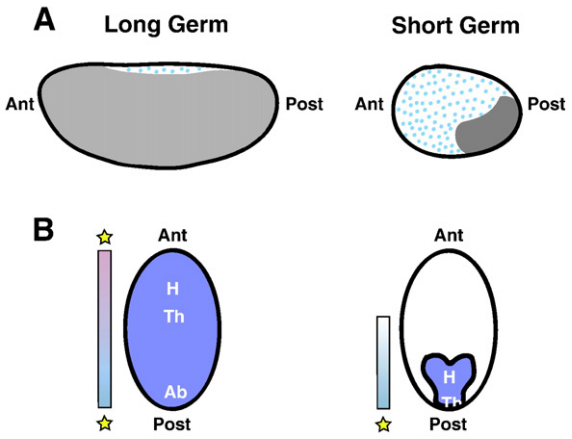

Fig. 1. Schematic representation of long germ and short germ embryos. (A) Lateral view. In long germ embryos, relatively little of the egg is allocated for extraembryonic tissues (blue dots), while the germ occupies the majority. The germ rudiment of short germ insects is restricted to the ventral posterior of the blastoderm, while the remainder of the egg is occupied by extraembryonic tissues. (B) Ventral view. In long germ insects, all of the future segments (head [H], thorax [T] and abdomen [A]) will be patterned in the precellular blastoderm by two patterning centers (indicated by stars). Short germ insects pattern only head and thorax before gastrulation, from a single patterning center at the posterior.

patterned at the syncytial stages. He called these insects "short germ", since the germ anlage represents only a few (the anteriormost) segments of the embryo, while the remaining (posterior) segments are generated via a posterior 'growth zone' after cellularization. Many were also "small germ", in reference to the relative small portion of the egg that serves as germ material (Fig. 1B). Short germ insects include the well-studied flour beetle, *Tribolium castaneum* (Coleoptera), the milkweed bug *Oncopeltus fasciatus* (Hemiptera), the cricket *Gryllus bimaculatus* (Orthoptera), and the grasshopper *Schistocerca americana* (Orthoptera). Differences between short and long germ insects may arise in part in the ovary where maternal information originates. It has been suggested that ovaries that possess nurse cells (meroistic ovaries), in contrast to the more ancestral panoistic ovaries, which lack them, may have been a critical intermediate in the progression from short germ development to long germ. The reliance of long germ embryogenesis on nurse cells to supply nutrients and determinants is largely supported [7] (The reverse is not necessarily true, as several short germ insects also possess meroistic ovaries.).

As there are orders of insects, such as Coleoptera, which possess members of both long and short germ types, this suggests that long germ embryogenesis was either lost in some short germ insects, or that it arose independently several times. This latter view is currently favored [8,9]. How did the transition(s) from short germ to long germ embryogenesis occur? The most informative approach to answering this question is to describe the long and short germ modes of development, and then revisit those aspects that have been transformed. We will begin with the best-described program: that of the long germ *Drosophila*.

2. Long germ embryogenesis: The *Drosophila* paradigm

Drosophila embryogenesis begins in the meroistic ovaries of the female (reviewed in [10]). The *Drosophila* oocyte is specified as one of 16 sister cells, the 15 others becoming nurse cells that will transcribe maternal messages encoding morphogens, as well as provide cellular machinery and mitochondria for the oocyte to develop rapidly. These are transferred into the oocyte via ring canals that connect the nurse cells and the oocyte. The nurse cells dump their contents into the oocyte, including mRNA's for several maternal factors that become localized to the poles of the oocyte. After fertilization, these mRNA's are translated and act as transcriptional or translational regulators. Syncytial nuclear divisions in the blastoderm embryo continue for 13 cycles, with the onset of the earliest zygotic transcription occurring around cycle 10, when the nuclei migrate out to the periphery of the embryo, with another wave during cycle 14 at the maternal to zygotic transition (MZT), when the nuclei become separated by cell membranes and the embryo becomes cellularized. By the end of cycle 14, the specification of the segments of the *Drosophila* embryo has largely been achieved.

The segmented *Drosophila* body plan is specified by a cascade of transcription factors that subdivide the embryo into increasingly small domains. In the late 1970's, large-scale saturation mutagenesis screens were carried out by Nüsslein-Volhard, Wieschaus, Schupbach and others to identify genes involved in segmentation [11,12]. The mutants identified in the screens were grouped according to the patterns of defects observed: genes required maternally for embryogenesis (maternal effect genes) that affect large regions of the body, like head, thorax, abdomen, or the non-segmented termini; genes that cause defects in groups of adjacent segments (gap genes); genes that affect alternating segments (pair-rule genes), and genes that affect every segment (segment polarity genes). These genes clearly act sequentially, patterning finer and finer regions of the embryo. The maternal effect genes, or *coordinate genes*, establish the initial polarity of the embryo, and initiate expression and position of the first zygotic genes, the gap genes, which act regionally in the embryo to regulate the downstream pair-rule genes. These, in turn, combinatorially regulate segment polarity genes in every segment, establishing the final number and boundaries of the segments. The identification of developmental genes allowed us to obtain one of the most precise descriptions of any complex biological system, the *Drosophila* embryo. It also provided the template to study how patterning of other animals is initiated, since the genes identified in *Drosophila* are among the first inroads made into the understanding of the embryogenesis of other insect (and vertebrate) models. A schematic representation of the patterns of expression of genes described in this section is provided in Fig. 2.

2.1. Maternal genes

Most maternal effect mutations affect genes whose messages are loaded by the mother into the oocyte to establish polarity in the early embryo (reviewed in [13–15]). These *coordinate genes* produce, for instance, the anterior determinant Bicoid (Bcd) [16] and the posterior determinant Nanos [17]). In early experiments in other Diptera, embryos were pricked at the anterior and the cytoplasm was permitted to leak out, resulting in embryos lacking the anterior structures— this indicated that instructive factors are contained in the cytoplasm at the poles of the oocyte of these species [18]. Indeed, the *bcd* and *nanos* mRNAs are localized to their respective poles using elements in their 3′ UTRs that allow the mRNA to be loaded onto cytoskeletal motors and transported to or trapped at the poles. The 3′ UTRs also mediate translational repression where protein product activity must be suppressed [19,20]. Both *bcd* in the anterior and *nos* in the posterior form strongly localized mRNA sources in the oocyte, which result in protein gradients during early embryogenesis. The localization of maternal messages is a critical step in establishing A-P polarity in embryos (see below). In contrast, mRNA of other maternal genes such as *hunchback* (*hb*) or *caudal* (*cad*) is loaded and evenly distributed throughout the early embryo [21] (see below).

bcd mutant mothers give rise to embryos that lack all anterior structures (head, thorax, and part of the abdomen) and have a duplicated posterior telson. However, the remaining abdominal segments retain proper polarity (reviewed in [14]). Bcd is a transcription factor that promotes anterior identity through the activation of zygotic *hb* expression as well as the expression of a