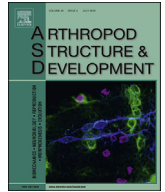




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Review article

Linking gene regulation to cell behaviors in the posterior growth zone of sequentially segmenting arthropods

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ABSTRACT

Virtually all arthropods add their body segments sequentially, one by one in an anterior to posterior progression. That process requires not only segment specification but typically growth and elongation. Here we review the functions of some of the key genes that regulate segmentation: Wnt, caudal, Notch pathway, and pair-rule genes, and discuss what can be inferred about their evolution. We focus on how these regulatory factors are integrated with growth and elongation and discuss the importance and challenges of baseline measures of growth and elongation. We emphasize a perspective that integrates the genetic regulation of segment patterning with the cellular mechanisms of growth and elongation.

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1. Introduction

The presence of repeated body segments is a defining feature of arthropods and has provided the key substrate for their evolutionary radiation. Nearly all of the millions of arthropod species develop their segments in the same fashion: they add them one by one from the posterior, in a region commonly called the “growth zone”. This sequential addition of segments during development is a well-known phenomenon in arthropods. Numerous classical studies describe the progressive nature of segmentation (Balfour, 1880; Kume and Dan, 1968; Anderson, 1973) as well as a posterior region of segment addition. It is surprising, therefore, that no clear model of “growth” in the growth zone ever emerged for arthropods. Posterior growth has been variously described as elongation, extension, growth, or proliferation, which, as Davis and Patel (2002) have noted, are all terms of “convenient ambiguity,” masking the fact that typically very little is actually known about this region. Indeed, the amount of growth the “growth zone” provides remains unknown for most arthropod embryos, a fact that has engendered a call to change the nomenclature from “growth zone” to the more neutral name of “segment addition zone” (Janssen et al., 2010). While segment addition is central to

sequential segmentation, cellular mechanisms of elongation – whether via cell division or otherwise – are also a critical part of segmentation and deserve to be highlighted since they co-occur with segment patterning. What mechanisms underlie elongation of the growth zone? Is cell division always required? How much cell movement occurs? While we currently lack data to provide answers to these questions, recent progress in both molecular genetics and live imaging of arthropod embryos promises a wealth of information to allow a more fine-grained analysis of the arthropod growth zone. Mechanisms of growth and elongation can now be analyzed with a careful examination of temporal dynamics, as well as spatial heterogeneity within regions of the growth zone. In addition, it is now possible to compare, and begin to link mechanisms that pattern segments and mechanisms that control growth and elongation. Finally, because of the growth of experimental tools that allow both cellular and molecular analysis in a broad sampling of arthropods, a rough picture of how the segmentation gene network evolved is emerging.

2. Overcoming conceptual biases based on *Drosophila* by taking a “growth zone” perspective

One of the features that fueled a renewed modern curiosity about mechanisms of sequential segmentation from posterior growth zones was the distinctive cellular context they exhibited compared to *Drosophila*, the best studied model of arthropod segmentation. In *Drosophila*, segments are patterned within a syncytial

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blastoderm by a cascade of interacting, diffusing transcription factors, giving rise almost simultaneously to all segments along the AP body axis (reviewed in Ingham, 1988; Nüsslein-Volhard and Wieschaus, 1980; Lawrence, 1992; Pankratz and Jäckle, 1993; St Johnston and Nüsslein-Volhard, 1992). By contrast, segments produced from posterior growth zones are operating within a fully cellularized environment and yet use many of the same regulatory molecules to pattern growth and segmentation (reviewed in Patel, 1994; Davis and Patel, 2002; Peel, 2004; Liu and Kaufman, 2005a; Peel et al., 2005). This contrast with *Drosophila* – however necessary because it is the source of the most well-understood segmentation mechanisms in arthropods – tends to obscure the great diversity of phenomena that are lumped under “sequential segmentation” in other arthropods. For example, a number of branchiopod crustaceans hatch from the egg as essentially a swimming head and subsequently add all their body segments (Anderson, 1973; Scholtz and Wolff, 2013). In these species, the growth zone occupies much of the trunk of the free-swimming hatchling larva, is covered by cuticle, and has poorly defined dorsal margins. In insects, by contrast, the growth zone is essentially a two-dimensional embryonic epithelium that lacks cuticle and possesses clear dorsal margins. In addition, even among insects the size of the growth zone and the number of segments sequentially specified is quite variable (Sander, 1981): for example, in the flour beetle, *Tribolium*, all segments posterior to mandible are added one by one (Brown et al., 1994), in the milkweed bug, *Oncopeltus* only the abdominal segments are added sequentially (Liu and Kaufman, 2003). These examples demonstrate the great variety among growth zones (see also reviews in Wanninger, 2015): occurring during larval versus embryonic stages, differing in size and number of cells, and specifying all versus few body segments. Indeed, the sheer variety of post-embryonic segment addition is widespread among arthropods, particularly myriapods (Minelli and Fusco, 2013). This variety highlights the disparate requirements of growth zones for posterior growth and elongation in different species and reflects the fact that cellular mechanisms of growth and elongation are likely a key substrate for evolutionarily diversification.

Another contrast when using *Drosophila* as a source of comparison for sequential segmenters is the relative shift in timing between segment patterning and segmental growth and elongation. *Drosophila* embryos undergo substantial amounts of elongation. However, germband elongation occurs *after* segment specification (e.g., Foe et al., 1993). In most other arthropod species, sequentially added trunk segments are specified *during* the process of elongation. This complicates the mechanistic dissection of segmentation and elongation, since cell division, cell movement and segmental patterning occur simultaneously in these species. This phenomenological integration of segmentation and elongation may or may not reflect a more fundamental integration of the gene regulatory networks that control the two processes.

In this review, we compare the diversity of growth zones by starting with an already formed growth zone, ignoring both the diversity of paths in the earliest stages of development that might produce it or the variable number of segments it might specify. We focus on features of growth zones that are most conserved and those which are likely to have been modified by evolution. We begin with a generalized overview of a growth zone. We then discuss known features of growth zone regulation, pointing out evolutionary variability within the common themes. We then review apparent links between cell behaviors underlying growth or elongation and regulatory processes patterning segment addition. Because these links between these two essential aspects of segmentation remain understudied, we review direct measures of growth zone cell behaviors. We conclude that there is little support for a *constant* engine of posterior growth/elongation: cell division

and cell movements demonstrate temporal variability. This lack of a steady state rate of segmentation suggests a similar rate variability in the underlying molecular mechanisms that drive segmentation. Finally, we discuss the challenge of understanding how segmentation and elongation are coordinated in sequentially segmenting arthropods. We postulate that the variation in the amount of cell division relative to cell movement is one of the key axes of evolutionary change between arthropod species.

3. A generalized view of an arthropod growth zone

We use the growing database of comparative analyses of how arthropods add segments to provide a sketch of an emerging model of common features in arthropod growth zones. We note from the outset that nearly all features of this model demonstrate variability within the clade, but use this generic model as an introduction to the more detailed discussion that follows. From a morphological perspective, a generic growth zone becomes identifiable after early stages of embryogenesis establish the initial embryo: after multiple rounds of cleavage, cells coalesce to form an initial embryo/larva with established anteroposterior (AP) and dorsoventral (DV) axes

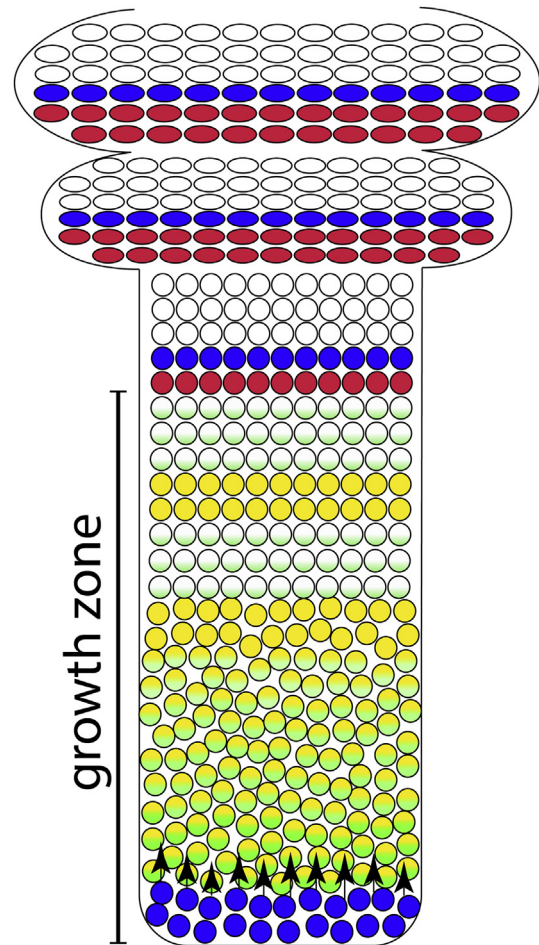


Fig. 1. Generic growth zone showing a posterior region of Wnt signaling (blue cells), a slightly anterior region of *caudal* expressing cells (green) showing a gradient of *caudal* expression from posterior to anterior. A posterior region of Notch and/or *eve* expressing cells (yellow) that resolves into transient stripes of expression. The anteriormost border of the growth zone expresses *engrailed* (red), that marks the posterior of each segment. Just anterior to that is Wnt expression in an adjacent stripe (blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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