

Hunting for “factor X”: the genetic basis of segmental mismatch

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Defending an evo-devo approach to the study of evolution in the pages of this journal may appear to be an unnecessary exercise. However, there are some case studies which, better than others, illustrate the necessity and the potential of considering developmental causes for explaining the evolution of organisms' body architecture. An example involving the evolution of segmentation in arthropods is the recent study by Janssen et al. (2008).

A zoology textbook would typically define a segmented animal as one whose body is composed of a series of modules (segments) that, more or less morphologically differentiated, are aligned along the main body axis. However, there are segmented animals in which such a modular composition is hardly recognizable, because different serial structures along the same axis of the same organism are repeated in discordant arrangement. This condition, termed “segmental mismatch,” characterizes the trunk of many arthropod taxa, in particular myriapods (millipedes, centipedes, and their allies), where the series of dorsal and ventral periodic structures (e.g., the dorsal sclerites and the leg pairs) do not match on a one-to-one basis (Fusco 2005).

In some millipede species, for instance, the number of leg pairs of a given individual cannot be inferred exactly from the number of the dorsal sclerites, and vice versa. Between the two numbers there is only a statistical correlation: about two leg pairs for each dorsal trunk sclerite (Enghoff et al. 1993). Neither is the matching between dorsal and ventral segmental series obvious in those millipede species where dorsal, pleural, and ventral sclerites are fused into a ring, because along most of the trunk there are two leg pairs for each ring, while the first three or four rings bear just one leg pair each. Actually, two different hypotheses for the correspondence between dorsal and ventral segmental structures had been competing for a while (reviewed in Janssen et al. 2006). One was based on what seemed to be the indisputable correlation between trunk sclerites and leg pairs in “ring-forming” species, as julids. The other was supported by descriptive embryological data, in particular by the relative arrangement of ventral and dorsal structures.

However, studying the expression of some segmentation genes in the pill millipede *Glomeris*, it finally turned out that

dorsal and ventral serial structures are independently established in the embryo, and that the boundaries of the prospective dorsal sclerites simply do not correlate with either the boundaries of the anlagen of ventral or dorsal structures (Janssen et al. 2004). Furthermore, while the ventral expression patterns of segmentation genes are practically identical to those known for *Drosophila* and other arthropods (Damen 2007), gene expression patterns in dorsal tissues are different. Ventral gene expression is congruent with the autoregulatory loop that in *Drosophila* establishes antero-posterior compartment boundaries (limits of clonal restriction), which involves Wingless-Hedgehog signaling, but dorsal segmental patterning must rely on a different system, as *wingless* is not expressed there. Janssen et al. (2004) postulated the existence of a “factor X,” partner of Hedgehog, which would functionally replace Wingless on the dorsal side.

Now, in a paper published in *Development, Genes and Evolution*, Janssen et al. (2008) unravel further details on the differences between dorsal and ventral segmentation in *Glomeris*, and, as is often the case in developmental biology, details matter.

Through a combinatorial study of expression data for a wider set of segmentation genes, the authors find evidence for a role of *decapentaplegic* as a substitute of *wingless* in establishing a boundary-forming regulatory loop on the dorsal side. However, far from being a simple replacement of one gene for another, eventually accomplishing the same task, this different signaling system not only involves a separate set of genes, but also entails a different polarity of the regulatory loop. In dorsal tissues, the boundary is posterior to the *eng-railed/hedgehog*-expressing cells, rather than anterior, and coincides with the posterior border of the prospective dorsal sclerite. Intriguingly, this dorsal signaling system is very similar to that described for the maintenance of compartment boundaries in the *Drosophila* wing disc (Shen and Dahmann 2005). The authors suggest that Hedgehog-Decapentaplegic signaling characterizes a gene cassette that could have been co-opted several times in evolution, to carry out similar functions in a variety of contexts.

Segmental mismatch is not taxonomically circumscribed, and the lesson we can learn from millipede development goes

beyond the limits of this particular animal group and a specific body axis. Janssen et al.’s study, while disclosing the developmental genetic basis for the dorso-ventral mismatch in millipedes, also sheds light on segmentation in the dorsal side of the embryo, the “dark side” of our current understanding of development in most arthropod model systems. Further, this study shows the value of a more development-based concept of segmentation, that applies to specific structural components of a body axis, rather than to the axis itself (Budd 2001, Minelli 2004, Minelli and Fusco 2004). In the study of evolution of segmental patterns, this concept allows abandoning the search for explanations based on the abstract logic of fusion or splitting of pre-existing segmental structures. The “tinkering” that produces phenotypic variation emerges at another level, at the level of the complex network of signals and regulatory interactions in development, that can produce either concordant or discordant segmental series, with the final effect of a modular body or a body affected by segmental mismatch, respectively.

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