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# Arthropod evolution and development: recent insights from chelicerates and myriapods

Daniel J Leite and Alistair P McGregor

Research on arthropod genetics and development has added much to our understanding of animal evolution. While this work has mainly focused on insects, a growing body of research on the less studied myriapods and chelicerates is providing important new insights into arthropod genomics and development. Multiple chelicerate lineages have a high incidence of gene duplication, which is suggestive of large-scale and even whole genome duplications. Furthermore, the duplication and divergence of genes is associated with the evolution of appendage morphology and other phenotypes in chelicerates and myriapods. Recent studies of these arthropods have also helped to understand the evolution and development of segmented bodies. Further research on chelicerate and myriapod models as well as species from other orders of these subphyla has great potential to expand our understanding of the evolution of animal genomes and development.

**Address**
Department of Biological and Medical Sciences, Oxford Brookes University, Gipsy Lane, Oxford OX3 0BP, UK

Corresponding author: McGregor, Alistair P (amcgregor@brookes.ac.uk)

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## Introduction

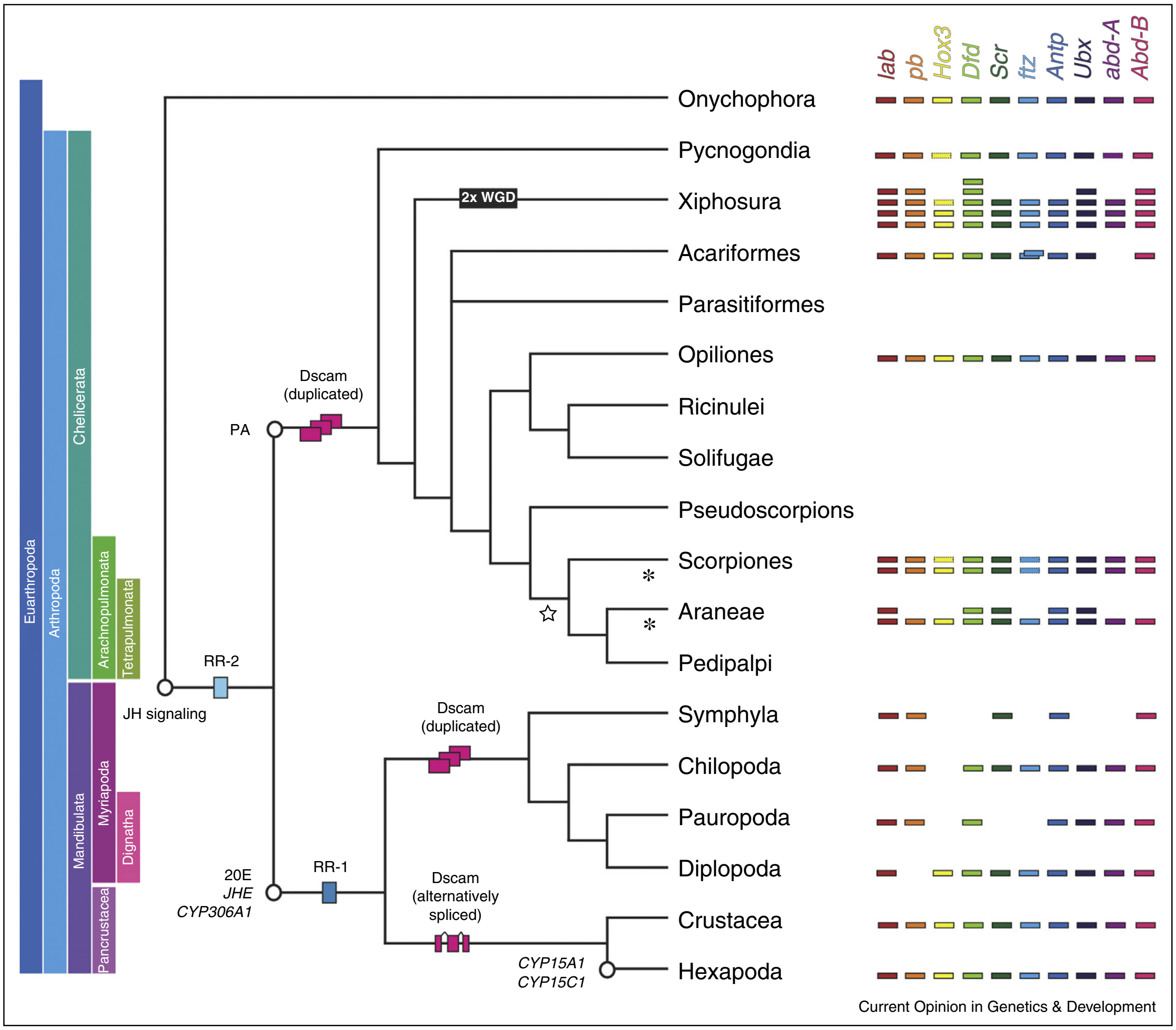
Recent studies of myriapods (e.g. millipedes and centipedes) and chelicerates (e.g. horseshoe crabs (HSCs), spiders, scorpions, and mites) have built on pioneering research to provide key insights into their developmental regulation and the evolution of development of arthropods and other metazoans. This work has predominantly utilized the geophilomorph centipede *Strigamia maritima* and the pill millipede *Glomeris marginata* as models to study myriapod embryogenesis [1] and powerful models, like the common house spider *Parasteatoda tepidariorum*, to study the genetic regulation of chelicerate development [2,3]. This work has relied on using *in situ* hybridization to study gene expression in these species [4–8], and in *Parasteatoda* both parental and embryonic RNA interference have been established to study gene function through global or clonal knockdown of gene expression respectively [9,10••]. Furthermore, sequencing of the first transcriptomes and genomes of myriapods and chelicerates has now also revealed the complete gene repertoires of some of these animals and informed our understanding of their evolution and development at a genomic level [11•,12,13,14•,15•,16]. Here we review recent advances in our understanding of phylogenetics, gene duplication, and the regulation of segmentation in chelicerates and myriapods, and highlighted outstanding questions to be addressed in these animals to further our understanding of animal development and evolution.

## Myriapoda and Chelicerata phylogenetics

It is now generally accepted that Chelicerata branch basally to the monophyletic Mandibulata (Myriapoda and Pancrustacea) in the arthropod phylogeny [14•,17,18,19•,20,21] (Figure 1). This is consistent with differences in gene content and expression that have been identified among these arthropods. For example, the development of the arthropod exoskeleton is regulated by cuticular proteins of the CPR family (Cuticular Proteins with the Rebers and Riddiford consensus). However, while the RR-2 subfamily of CPR genes is present in all arthropods, the RR-1 subfamily is restricted to the Mandibulata [14•,16,22,23] (Figure 1). Furthermore, particular components of the juvenile hormone signaling pathway are restricted to hexapods (CYP15A1/CYP15C1) or mandibulates (JHE and CYP306A1), and chelicerates likely use ponasterone A (25-deoxy-20E) rather than 20-hydroxyecdysone (20E) as their main molting hormone [13,15•,24] (Figure 1). In addition, the expression of *cap-n-collar* differs between chelicerates and mandibulates, and is associated with the evolution of the mandibles in the latter [25].

While the relationships of the arthropod subphyla appear to be resolved, reconstructing a robust Chelicerata or Myriapoda phylogeny has remained challenging. In Myriapoda, it is thought that the Symphyla are a sister group to the other classes, and that the Dignatha clade (Pauropoda and Diplopoda) are monophyletic [20] (Figure 1). In the Chelicerata, recent molecular evidence supports the Tetrapulmonata (Pedipalpi and Araneae), and Arachnopulmonata (Scorpiones and Tetrapulmonata) [18], but not consistently the Poecilophysidea (Solifugae and Acariformes) [17,18] (Figure 1). Resolving the phylogenetic relationships of orders within these arthropod subphyla is

**Figure 1**




**Phylogeny and Hox repertoire of chelicerates and myriapods.**
Juvenile hormone signaling was likely present in the common ancestor of arthropods. Changes in the components of the JH pathway, such as the mandibulate specific CYP306A1 and JHE, have lead to divergence in signaling between chelicerates and myriapods. *Dscam* genes (pink boxes) are expanded in copy number in chelicerates and myriapods, but *Dscam* is alternatively spliced to generate extensive isoform diversity in pancrustaceans. The cuticular proteins RR-2 (light blue box) are found across arthropods, but RR-1 genes (dark blue box) are restricted to mandibulates. The Hox gene repertoires are shown for each clade. Boxes with dotted outlines indicate variation in the presence or absence between species within a clade. Two whole genome duplications (2× WGD) have been proposed in HSCs. It is possible that scorpions and spiders have undergone independent large-scale duplications (asterisk), or a shared duplication in the Arachnopulmonata ancestor (star). JH, juvenile hormone; PA, Ponasterone A; 20E, 20-hydroxyecdysone. Phylogeny based on [2], and Hox gene repertoires from [14•,15•,16,28–32,34•,35,36,93,94].

important to inform our understanding of the evolution of differences between lineages as well as similarities that may provide evidence of the ancestral aspects of their genetics and development.

## Gene duplication in Chelicerata and Myriapoda

Gene duplication is an important mechanism for the generation of organismal diversity [26,27]. Genomic and transcriptomic sequencing for a number of myriapod and chelicerate species has revealed interesting patterns of gene duplication in these animals and we are beginning to understand how this has contributed to their evolution.

### Gene duplication in chelicerates

Several chelicerates exhibit pervasive gene duplication. In *Parasteatoda* 28% of annotated transcripts are expressed from duplicated genes [12] and duplicates of some Hox genes have been found in this spider and in *Cupiennius salei* [7,28,29] (Figure 1). Furthermore, there is