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## 18.1 Introduction

By many metrics, arthropods constitute one of the most successful animal phyla on our planet, manifest in extreme species richness, enormous diversity in morphologies and developmental modes, and successful radiation into nearly every inhabitable ecological niche available to multicellular organisms (Storch and Welch 1991; Brusca and Brusca 2002; Ødegaard 2000; Valentine 2004; Gullan and Cranston 2004; Grimaldi and Engel 2005). In this chapter, we will explore some of the causes and mechanisms that have enabled arthropod diversification. We define evolvability broadly as a lineage's capacity to generate phenotypic diversity over evolutionary time. We begin by exploring two prominent axes of diversification in the arthropods: evolvability in (1) developmental space and in (2) developmental time, and their respective contributions to facilitating innovation, diversification, and radiation within the Arthropoda. We end our chapter by examining the role of (3) developmental plasticity in arthropod evolution. In each context, we explore the genetic, developmental, and ecological mechanisms that may have allowed arthropods to diversify more than any other group of animals, the interactions among these mechanisms, and the emergent properties of these interactions. Throughout, we highlight key questions for future research, in particular as created by

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the increased integration of evolution and ecology with developmental biology and genomics.

## 18.2 Evolvability in Developmental Space

The first major axis of arthropod evolution examined in this chapter concerns the diversification of body regions, segments, appendages, and other morphological “units”. The early Cambrian arthropods already exhibited the characteristics that have come to define the group (Conway Morris et al. 1987; Hou et al. 2004) among these being meristic subdivision of the exoskeleton into distinct appendage-bearing segments. Among the most important themes in arthropod evolution is the specialization of these individual segments and segment groups and of the corresponding outgrowths they bear.

### 18.2.1 Redundancy in Arthropod Body Architecture

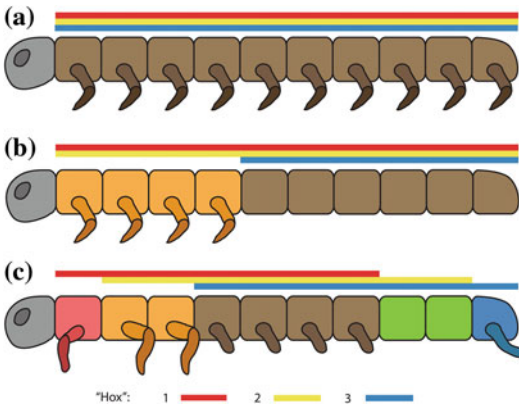
The ancestral arthropod is often represented as possessing a trunk composed of externally homonomous segments, each bearing an undifferentiated pair of appendages (Akam et al. 1988). The precise organization of the protoarthropod remains to be fully elucidated, but what is clear is that it represented an evolutionary ground state endowed with vast potential for diversification (=evolvability), realized in extraordinarily varied arthropod morphologies. This potential appears rooted, at least in part, in the compartmentalization of repeating morphological units and in the redundancy inherent in such a body plan. Redundancy is integral to diversification across levels of biological organization (reviewed in Galis and Metz 2007). For instance, the evolution of new genes and gene functions is thought to be greatly facilitated by gene duplication events, which allow one copy to undergo modification while the other retains the ancestral function (Ohno 1970; Force et al. 1999). Similarly, an ancestral organism

composed of multiple morphological units of similar function may be deconstrained evolutionarily to a degree roughly proportional to the level of redundancy present in the system *provided one critical condition is met: that reiterated units can be developmentally decoupled*. In such a system, individual segments are afforded some measure of low-risk mutational and developmental exploration because neighbouring units continue to carry out crucial locomotory or food manipulation functions. Arthropod evolution is replete with examples of differential segment evolution giving rise to dramatic divisions of labour between neighbouring body regions. Segmental redundancy may thus have deconstrained the diversification of individual segments at a functional/anatomical level, facilitated by the genetic decoupling of segments into quasi-independent developmental units.

### 18.2.2 Compartmentalization of Arthropod Development: Genetically Decoupled Units

The evolutionary independence of morphological units is, of course, reliant upon a developmental system that is subdivided and decoupled in space. Because the diversification of segments and the appendages they bear is perhaps the most important theme of arthropod evolution, we focus our attention initially on the Hox genes. Hox genes encode highly conserved transcription factors that regulate segment identity along the anterior–posterior axis (Lewis 1978; Akam 1989). In other words, regions expressing unique suites of Hox genes (and other transcription factors) define quasi-independent developmental/evolutionary units, allowing downstream genetic programs to be activated or deactivated differentially based on spatial position.

Morphological units—in this case, segments or segment groups and their corresponding outgrowths—can thus diverge to a level permitted by the underlying genetic architecture (Fig. 18.1), such as Hox gene expression (Angelini and



**Fig. 18.1** The principle of developmental decoupling and resolution of segment identity mediated by three Hox-like protein domains in three hypothetical arthropod-like embryos (note that these examples are not meant to represent actual species or hypothetical ancestral states). In “Species a”, all three proteins are expressed over the entire length of the trunk defining this entire region as a single morphological unit. Appendage modifications are expected to affect all segments more or less equally. “Species b” has undergone a shift in the expression of “Hox 3”, delineating two broad “tagmata” in the trunk. Note that homologous Hox expression profiles need not specify similar phenotypic states across lineages (overlapping domains of Hox1, 2, and 3 interact to repress appendage formation in “Species b” in contrast to “Species a” where they merely modify limb identity). The Hox domains in “Species c” are maximally offset relative to each other and therefore allow the greatest number of distinct segment-group identities possible in a 3-gene system with continuous Hox expression domains [ $2n - 1$  distinct regions possible where  $n = \#$  of Hox genes (Angelini and Kaufman 2005a)]. Note that the Hox expression profile represented in “Species c” is not common in nature and that real arthropods generally exhibit far fewer distinct segment identities than are theoretically allowed by simple Hox combinatorics (Minelli 2003)

Kaufman 2005a). For example, insects and myriapods differ markedly in the degree to which they have undergone morphological specialization of locomotory appendages. While myriapod walking legs have remained essentially uniform throughout their history, diverse insect orders have independently recruited individual pairs of thoracic legs for highly specialized roles such as food acquisition (mantids), jumping (orthopterans), digging (mole crickets), swimming (water boatmen), etc. This discrepancy is likely

explained, in part, by the differing degrees of developmental resolution imparted by Hox gene expression in the two groups. Insects have three segments that bear locomotory appendages, each of which lies within the domain of a unique combination of Hox genes—prothorax, *Sex combs reduced (Scr)/Antennapedia (Antp)*; mesothorax, *Antp*; and metathorax, *Antp/Ultrabithorax (Ubx)* (reviewed in Hughes and Kaufman 2002a). This bestows a distinct developmental identity and corresponding evolutionary degree of freedom to each insect thoracic segment as expression of downstream patterning genes can be activated, inhibited or modified within a given segment without affecting expression in other domains. In contrast, the locomotory segments of myriapods are regulated by a pair of broadly expressed Hox genes, *Ubx* and *abdominal-A (abd-A)* (Hughes and Kaufman 2002b). This genetic unity may underlie an evolutionary developmental indivisibility that precludes morphological and functional differentiation among walking legs of the myriapod lineages relative to those of the insects.

As Hox genes define segment identities and delineate domains of tagmatization, marked evolution of arthropod body organization may also be enabled through relatively simple shifts in the domains of Hox expression. Averof and Patel (1997) showed that, similar to myriapods, the locomotory tagma in some crustaceans is induced by the broad expression of posterior Hox genes. In some lineages, a variable number of the thoracic appendages have been modified for feeding—termed maxillipeds. The researchers found that the anterior reach of the *Ubx/abd-A* domain had shifted 1, 2, or 3 segments posteriorly, corresponding to the number of maxilliped pairs displayed by each group, respectively. This demonstrates the flexibility of the arthropod body plan as abrupt changes in the character of units—and therefore in the organization of the body plan and ecological strategies—are possible through relatively simple genetic modifications. These results may also suggest that the character of morphological units may be deconstrained when placed in a new regulatory context.

### 18.2.3 Compartmentalization of Arthropod Development: Semi-Autonomy of Gene Networks

It is important to point out that while Hox genes, through segment-specific activation or repression of various effector genes, can modify the character of the resultant appendage (or, in many cases, interrupt its expression entirely), the machinery associated with appendage induction *per se* is independent of Hox control in arthropods. This adds to the evolutionary flexibility of the system because domain-specific development does not require the evolution of novel pathways or genes for each domain. Instead, only patterns of activation, inhibition, and integration must be segment specific, whereas the genes and their products whose expression is modified in a domain-specific manner can themselves remain conserved. As a consequence, diversification is facilitated through changes in assembly, rather than changes in component parts.

The core components underlying the patterning of appendages are largely conserved in arthropods (reviewed in Angelini and Kaufman 2005b) and, to a lesser degree, throughout the animal kingdom (Panganiban et al. 1997). Much research in appendage induction has focused on the orthologs of the homeodomain-containing transcription factor, *Distal-less* (*Dll*), which activates the formation of the proximo-distal appendage axis (Cohen et al. 1989). *Dll*, in turn, is activated by signals that are present on each trunk segment, while Hox-mediated signals act in parallel, transmitting instructions to modify the appendage in a domain-specific manner (reviewed in Morata 2001). In many arthropod groups, Hox genes have evolved the capacity to inhibit the expression of *Dll* entirely—such as *abd-A* in insects (Vachon et al. 1992; Lewis et al. 2000) and *Antp* in arachnids (Khadjeh et al. 2012)—resulting in the characteristically legless abdomen (or opisthosoma). However, because the developmental machinery of appendage patterning is maintained independent of these repressive

signals, trait recurrence is possible in body regions where the expression of that trait has previously been dormant. This potential has been demonstrated experimentally, where inhibiting the repressive effects of a single gene results in the ectopic recurrence of appendages on previously limbless body regions (Lewis et al. 2000), and also in nature, as in the case of caterpillar prolegs. Lepidopteran caterpillars exhibit functional pairs of appendages on five of their abdominal segments. Warren et al. (1994) showed that this feat is accomplished developmentally through segment-specific inactivation of the appendage-repressive *abd-A* gene. This secondary lifting of inhibition allows the ancestrally dormant yet conserved appendage-patterning network to be reactivated, resulting in the formation of abdominal limbs. In some extreme cases, reappearance of traits may be associated with such profound phenotypic modification that they may be considered true evolutionary novelties. For example, Prud'homme et al. (2011) presented intriguing developmental and anatomical evidence that the pronotal helmets of membracid treehoppers may be derived from the long-repressed T1 wing homologue (but see Miko et al. 2012; Kazunori 2012).

While the reactivation of conserved gene networks within their ancestral context can contribute to the reappearance of dormant phenotypes, the “reuse” of these signals outside of the confines of strict homology has the potential to create truly novel traits. Because the networks underlying various traits are integrated, self-contained units that may be induced by relatively few signals, they can theoretically be wired readily into other regulatory circuits and thus expressed in novel developmental and anatomical contexts. A well-known experimental example is the ectopic expression of the *Drosophila eyeless* gene. The *eyeless* induction in foreign domains such as legs or wings is sufficient to result in the ectopic formation of well-organized ommatidia in these body regions (Halder et al. 1995), illustrating the potential ease with which entire developmental-genetic modules can, in principle, become functionally co-opted into novel developmental contexts.

Such co-option may underlie much innovation in arthropod evolution. For instance, gene networks traditionally associated with appendage formation appear to have been co-opted repeatedly into novel contexts, facilitating for instance the evolution of beetle horns (Moczek and Nagy 2005; Moczek and Rose 2009; Wasik et al. 2010), which, though not homologous to appendages, at least share many of the same properties, or the foci of butterfly wing eyespots, whose similarities to conventional appendages appear far more remote (Carroll et al. 1994). A high degree of evolvability may thus be expected in biological systems that possess (a) traits underlain by modular gene networks under relatively simple regulatory control, and (b) a flexible regulatory scaffold into which these conserved networks can be wired in diverse ways.

In summary, arthropods are endowed with anatomical and developmental qualities that may make them particularly amenable to morphological change. The early organization of the arthropod body plan into a series of morphologically similar and functionally redundant units was likely a key step in predisposing the Arthropoda to evolutionary malleability. The extent to which exploration of morphological space was possible within segments and segment groups relied critically upon the degree of spatial decoupling present in the underlying genetic architecture. The flexibility of the system was further facilitated by the modular nature of gene networks under relatively simple regulatory control, enabling their transfer across a flexible regulatory scaffold by means of modest developmental-genetic modifications.

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### 18.3 Evolvability in Developmental Time

The second major axis of diversification we examine concerns the evolvability of arthropods in developmental time, along the life cycle of individuals. Immature and mature stages, with or without distinct transitional forms, have evolved to varying degrees in different groups of

arthropods (Storch and Welch 1991; Mente 2008; Grimaldi and Engel 2005). In many ways, these are best understood from studies on hexapods (Nijhout 1994, 1999a). Here, developmental modes range from ametabolous (continued moulting throughout adult life with no metamorphosis except for the addition of genitalia, e.g. silverfish) to hemimetabolous (terminal adult moult; more or less gradual transformation of immature into adult; metamorphic addition of wings and genitalia, e.g. cockroaches and grasshoppers) to holometabolous development (terminal adult moult; complete transformation of immature into adult via the intercalated pupal stage; e.g. beetles and butterflies). A similar diversity of developmental modes is also observed, though much less well understood, in the crustaceans, ranging from direct, largely ametamorphic development seen in groups such as the ostracods or cladocerans to highly disparate larval and transitional stages found in the life cycles of many Eucarida (Brusca and Brusca 2002; Mente 2008).

In all of these cases, parts of the life cycle have evolved more or less distinct identities, enabling them to diversify and specialize to varying degrees independently from other parts. Thus, like segments along the body axis, different stages in the life cycle have evolved increased modularity, with important consequences for the evolutionary and ecological success of many arthropod lineages, such as the origin of true larval stages with distinct ecologies and the evolution of metamorphosis in the Holometabola. Below, we discuss some of the mechanisms underlying this ontogenetic modularity, their origins, interactions and emergent properties, and their ability—by themselves, as well as in interaction with the mechanisms underlying spatial modularity discussed above—to foster innovation and diversification.

Before doing so, however, we would like to emphasize that the developmental decoupling of different life stage as discussed below, just like the developmental decoupling of adjacent segments or groups thereof discussed above, is of course not absolute, instead it is relative (for insightful discussions of these points see Minelli 2003, 2009;

Scholz 2004; Minelli et al. 2006, and references therein). Pleiotropic constraints may be reduced, but certainly not eliminated. Rather than pearls on a string that can be exchanged, added or lost, stages and body regions remain complex phenotypes whose development and existence *enable*, *and as such constrain*, subsequent stages and adjacent body regions, respectively. This is particularly important if we seek to homologue temporal and spatial developmental modules in phylogenetic studies (Minelli et al. 2006), or seek to infer causes or consequences of developmental evolution between associations and constellations of modules (Scholz 2004). Lastly, where one stage (or body region) ends and another begins is a non-trivial issue to consider when studying, comparing, and interpreting arthropod development (Minelli et al. 2006). For example, while the moulting cycle provides a convenient periodization of arthropod development, developmental, and physiological processes may vary greatly in the degree to which this periodization matters to their actions during each intermoult. Similarly, much developmental disparity may occur *within* traditional stages, as in late holometabolous larvae entering the prepupal stage (Nijhout 1994) or the induction of diapause during portions of larval or pupal development (Denlinger 2002). As such, boundaries between modules may or may not coincide with our preconceived notions. With these caveats in mind, however, we believe that thinking of arthropod development as being composed of, at least in part, temporal and spatial modules that can develop to varying degrees independent of each other, provides a valuable starting point for investigating how spatial and temporal modularity, by themselves and in interaction, may delineate the evolutionary degrees of freedom exploitable by an evolving lineage.

### 18.3.1 Mechanisms

The expression of, and transition between, distinct life stages requires mechanisms that specify life stage identity and order. Here, endocrine mechanisms play a key role in communicating throughout the body of a developing arthropod

what kind of stage in the life cycle to express, and when to transition to the next stage. A detailed presentation and discussion of arthropod endocrine mechanisms is given in [Chap. 6](#) of this volume (Nijhout 2013). Here, we would like to briefly highlight and expand on a subset of issues, best understood through the study of insect development and metamorphosis.

In holometabolous insects, that is, insects that possess a distinct larval stage that transforms into the final adult via a larval-to-pupal and pupal-to-adult moult, the interplay between ecdysteroids and juvenile hormone orchestrates whether moults maintain the current developmental *status quo* (as in a larval-to-larval moult) or lead to the transition to a new stage (as in the larval-to-pupal and pupal-to-adult moults; reviewed in Nijhout 1994, 1999a; Truman and Riddiford 2002; Wheeler and Nijhout 2003). As such, the endocrine control of moulting and metamorphosis effectively subdivides the developing organisms into distinct temporal domains free to utilize, inhibit, or differentially integrate developmental pathways independent of other temporal domains. As a consequence, stage-specific gene expression and modulation of pathway activity are ubiquitous, enabling the promotion of larval-specific features during larval development (such as abdominal prolegs or feeding mandibles in caterpillars), their destruction (prolegs) or transformation into adult structures (feeding mandibles to proboscis) during the pupal stage, as well as the origin of adult-specific structures in late larval and pupal development (e.g. wings and genitalia; Chapman 1998; Heming 2003). Similarly, stage-specific activation of developmental and physiological processes underlie many ontogenetic diet shifts observed across holometabolous life stages, such as in mosquitoes (which switch from detritus-feeding in larvae to blood-(females) or pollen-feeding (males) in adults; Marinotti et al. 2006; Koutsos et al. 2007), or butterflies, (which switch from leaf feeding in caterpillars to nectar feeding in adults; Chapman 1998; Heming 2003; see also Rabossi et al. 2000). Much like spatial modularity discussed above enables adjacent segments to express very different morphologies

or produce highly disparate appendages, stage-specific modularity in gene expression and pathway activation facilitates niche-specific adaptation while reducing pleiotropic constraints. Furthermore, as with segment-specific development, stage-specific development does not require the evolution of new genes or pathways: instead, only patterns of activation, inhibition and integration must be stage-specific whereas the genes and their products whose expression is modified can themselves remain conserved. Again, diversity is facilitated through changes in assembly, rather than changes in component parts.

### 18.3.2 Ontogenetic Modularity and Speciation

If ontogenetic modularity facilitates diversification, we would predict that lineages with relatively more modular development should diversify more readily. The most rigorous examination of this basic hypothesis comes from a study by Yang (2001), which compared rates of diversification and extinction at the family level across hemi- and holometabolous insect orders. Insects represent as close to an ideal set of taxa for this purpose as hemi- and holometabolous insect orders differ predominantly in developmental modes, that is, the absence/presence of an elaborate larval and distinct pupal stage, but not in tagmatization or other confounding issues that may complicate comparisons among many other arthropod taxa. One important complication nevertheless remains: hemimetabolous insects constitute a paraphyletic group, with the hemimetabolous Eumetabola (thrips, true bugs, lice, and book lice) being more closely related to the Holometabola than to the remaining Hemimetabola. Taking this factor into account, Yang (2001) calculated family-level rates of diversification from the fossil record and found that Holometabola exhibited a significantly and characteristically higher rate of diversification compared to the less modular Hemimetabola as a whole, or Eumetabola if

analysed separately. Importantly, analyses of survivorship curves for families of the Hemi- and Holometabola found no differences in extinction rates, suggesting that differential diversification, not extinction, underlies the relative taxonomic success of the Holometabola (Yang 2001). Compatible analyses have yet to be conducted in other arthropod lineages, though similar patterns may emerge there as well. For instance, crustacean lineages differ widely in developmental modes, with the most extreme degree of disparity among life stages seen in the Malacostraca, which also happens to represent one of the most species-rich crustacean lineages (Mente 2008; Regier et al. 2010).

Taken together, existing data clearly support the hypothesis that intrinsic differences in ontogenetic modularity influence the long-term diversification rates of lineages. Intriguingly, the same hypothetical framework makes an additional prediction, namely that characters in more ontogenetically modular clades should exhibit greater levels of variation due to their enhanced temporal independence. To date, this key prediction remains untested.

### 18.3.3 Ontogenetic and Spatial Modularity, Diversification and Innovation

Stage-specific modularity interacts with spatial modularity discussed above, allowing not only different body regions to develop independently of each other, but the “same” body region to develop very differently during different stages of the same life cycle. It is a characteristic feature of the holometabolous insects that hardly any body region or appendage looks remotely similar when larval (think maggot, caterpillar, grub) and adult (think fly, butterfly, beetle) stages of the *same* individual are compared. But the contributions of spatial and ontogenetic modularity to evolvability likely go even further, for instance when a formerly stage-restricted trait becomes expressed in a different stage in the same or different location. When this occurs,

truly novel traits may originate, but may do so at least initially with modest developmental-genetic modifications (Fig. 18.2).

For example, all pupae in the extremely species-rich scarab beetle genus *Onthophagus* express more or less conspicuous thoracic horns (Fig. 18.2 top panel). A combination of histological and functional studies shows that these horns function as moulting devices, enabling the shedding of the highly sclerotized larval head capsule during the larval-to-pupal moult (Moczek et al. 2006). In the majority of species, these thoracic horns are resorbed during the pupal stage through programmed cell death (Moczek 2006; Kijimoto et al. 2010). Males of some species, however, convert this pupal outgrowth into a corresponding adult horn, which is then used as a weapon in male combat over access to females. Phylogenetic analyses strongly suggest that the moulting function of pupal horns predates the weapon function of adult horns (Moczek et al. 2006). This raises the possibility that adult thoracic horns, a novel trait lacking obvious homology to other insect structures, may have originated through the simple failure to remove a pupa-specific structure. Intriguingly, similar resorption failures occur in natural populations of thoracic-hornless species at a low but detectable frequency (Moczek et al. 2006; Kijimoto et al. 2010). More generally, this example illustrates how ontogenetic modularity enabled the evolution of an originally pupal-specific trait, which, once transferred into a new developmental stage, facilitated the rapid evolution and diversification of a novel trait and function, in this case that of a weapon of sexual selection.

A second example is illustrated by the bioluminescent photic organs in fireflies (beetle family Lampyridae, Fig. 18.2 bottom panel), which are thought to have originally evolved as a larval-specific trait (Branham and Wenzel 2003) likely used to generate aposematic signals to predators (De Cock and Matthysen 1999). While all known larval lampyrids develop photic organs, only a subset of lampyrid lineages also develops the more derived adult organ (Branham and Wenzel 2003). Although adult organs are similar to larval organs in the sense that both

emit light, they are not strictly homologous. Adult organs are more intricately organized, develop in different abdominal segments, and do so even when the larval organ is ablated experimentally (Harvey and Hall 1929). However, both organs derive from the same cell population, the fat body (Hess 1922), and utilize many of the same biochemical processes. Here, ontogenetic and spatial modularity appear to have facilitated the partial carry-over of a larval-specific trait into a different developmental stage, where it now functions in a completely different and novel context, the attraction of mates and, occasionally, of prey (Lloyd 1965).

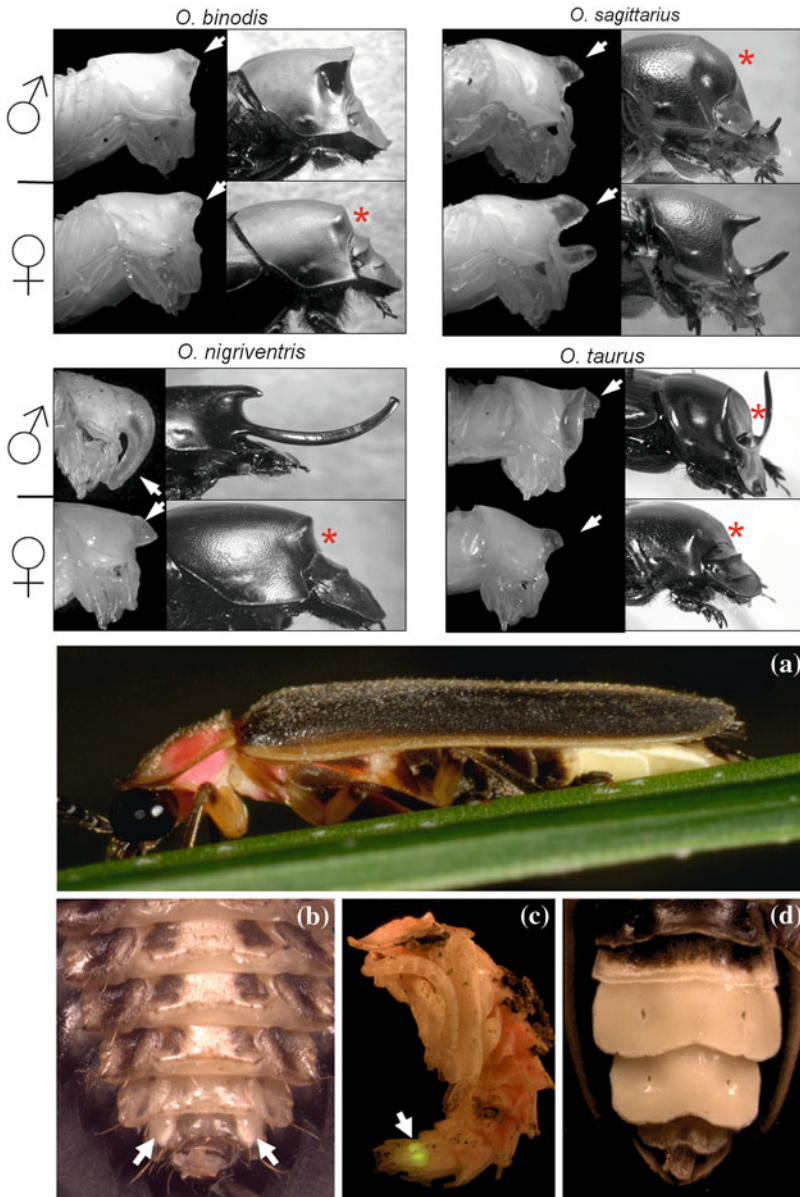
In summary, ontogenetic modularity allows different life stages of the same life cycle to develop and evolve, partly independently of each other, thereby elevating the long-term diversification rates of lineages. Through its interactions with spatial modularity, it enables the “same” trait to develop very differently in different stages of the same individual, adding evolutionary degrees of freedom to evolving lineages. Lastly, by itself as well as in combination with spatial modularity, ontogenetic modularity can result in the transfer of stage-specific traits to new stages within the same life cycle, thereby creating complex novel traits with modest developmental-genetic means.

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## 18.4 Evolvability through Developmental Plasticity

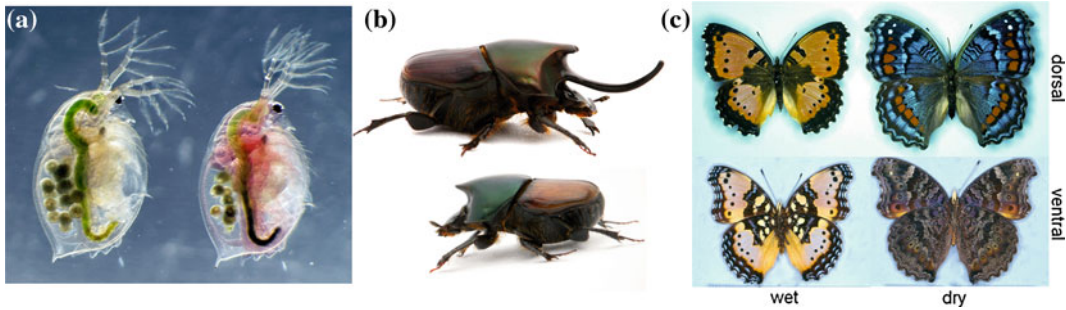
In this last section, we would like to step back from the two major axes of diversification examined above—developmental space and time—and towards a more universal property of all development—plasticity—and examine its contribution to arthropod evolvability. Developmental plasticity can be defined as a single individual’s ability to adjust patterns of phenotype expression in response to changes in environmental conditions. Virtually all organisms as well as biological processes exhibit some degree of plasticity (West-Eberhard 2003; Whitman and Ananthakrishnan 2009). On one extreme, such effects may arise simply from the biochemical





**Fig. 18.2** Two examples of innovation and diversification enabled through the interplay of spatial and ontogenetic modularity. (*Top panel*) Thoracic horn in the beetle genus *Onthophagus*. Shown are pupal and adult morphologies of males and females of four species. All pupae in the genus express conspicuous thoracic horns (marked by *arrow*), which play a critical role in the shedding of the highly sclerotized larval head capsule during the larval-to-pupal moult (Moczek et al. 2006). In the majority of species, these thoracic horns are resorbed during the pupal stage through programmed cell death (marked by *asterisks*) and regardless of sex, as exemplified by *O. taurus* (Moczek 2006a; Kijimoto et al. 2010). Males in a subset of species (shown here for

*O. binodis* and *O. nigriventris*), however, convert this pupal outgrowth into a corresponding adult horn, which is then used as a weapon in male combat over access to females. In one highly unusual species (*O. sagittarius*), these sex-roles are reversed. See text for further description. (*Bottom panel*) Photic organs, or lanterns, of two firefly genera in the beetle family Lampyridae. Shown are (a) an adult *Photinus* firefly as well as close ups of *Photuris* larval (b), pupal (c), and *Photinus* adult (d) photic organs (note that larval/pupal lanterns are located on abdominal segment VIII (A8) in most lampyrids while the lanterns of adult males of both *Photinus* (shown) and *Photuris* (not shown) occupy A6-7). See text for further description



**Fig. 18.3** Three examples of developmental plasticity in which environmental conditions mediate extensive reorganization of development. **a** When the water flea *Daphnia magna* is confronted with poor oxygen concentrations, it increases haemoglobin concentration in the haemolymph by a factor of 15–20, colouring the body red (images by Dr. Shin-ichi Tokishita, Tokyo University of Pharmacy and Life Sciences). **b** Good or poor larval feeding conditions cause male horned beetles of many species (here *Onthophagus nigriventris*) to develop into

distinct horned and hornless morphs, respectively, which in turn employ distinct fighting and sneaking reproductive behaviours (images by Alex Wild). **c** The Gaudy Commodore, *Precis octavia*, expresses alternative wing colours and pattern arrangements depending on season. Note that dorsal (**c**, left) and ventral (**c'**, right) wing surfaces adjust their development to season completely independent of each other, representing a striking example of the interactions between spatial modularity and developmental plasticity (images by Fred Nijhout)

and biophysical dependencies of developmental processes, for example, the temperature dependence of enzymatic reactions or the pH-dependent folding of proteins (Schlichting and Pigliucci 1995). On the other extreme are highly choreographed responses to environmental changes such as nutrition-dependent modification of growth and reproduction, physiological responses to temperature shock or oxygen deprivation, caste formation, seasonal migration, learning, and many more (Fig. 18.3). Here, plasticity represents a complex, evolved response that enables developing organisms to maintain high fitness in the face of environmental variability (Schlichting and Pigliucci 1998; Nijhout 1999b, 2003; West-Eberhard 2003). Lastly, plasticity also underlies many homeostatic responses and canalization in development (Scharloo 1991), that is, processes intended to achieve phenotypic constancy, at least on specific levels of biological organization. From minimizing fluctuations in blood sugar levels in the face of nutritional variation to the maintenance of proper scaling relationships of body parts during growth, organisms flexibly adjust a vast array of plastic processes on some levels of biological organization to ensure phenotypic constancy on others (Moczek 2010). In

the next section, we would like to highlight the means by which developmental plasticity in its various manifestations contributes to evolvability in general, and how it might have done so specifically during the diversification of certain arthropod lineages.

#### 18.4.1 Contributions of Developmental Plasticity to Diversification and Innovation in Arthropods

Developmental plasticity is believed to contribute to organismal innovation and diversification through a diversity of mechanisms operating on a variety of levels of biological organization (Pfennig et al. 2010; Moczek et al. 2011). For instance, developmental plasticity is predicted to facilitate colonization of novel environments, thus increasing the likelihood of adaptive radiations and speciation events. While studies on fish and amphibians support this prediction (Pfennig and McGee 2010), no complementary studies have been conducted to date on any arthropod lineages.

Developmental plasticity is also predicted to facilitate diversification by providing additional targets, such as the developmental, genetic, or

endocrine machinery underlying plastic responses, for evolutionary processes to act on. Here, much evidence exists from studies on diverse arthropods that illustrate that the nature of plastic responses can evolve, diversify, and mediate population divergences independent of trait means in different environments (e.g. lacewings: Tauber and Tauber 1972; beetles: Moczek and Nijhout 2002; pitcher-plant mosquitoes: Bradshaw et al. 2003; cabbage-white butterflies: Snell-Rood and Papaj 2009; water fleas: Scoville and Pfrender 2010).

Similarly, developmental plasticity is predicted to enhance modularity of development by providing reusable building blocks for the regulation of diverse development contexts. Several interesting examples exist in insects that suggest that much diversification, and in fact several key innovations, may have been facilitated through the repeated co-option of the same plastic regulatory processes into different contexts (reviewed in Nijhout 1994, 1999a, b, 2003). For instance, in holometabolous insects, the same endocrine machinery coordinates alternative reproductive decisions (whether to invest into growth or reproduction), alternative developmental decisions (moulting and metamorphosis), as well as decisions between alternative phenotypes (facultative diapause, host switch, caste, and morph expression).

Intriguingly, certain types of developmental plasticity may selectively enable the accumulation of genetic variation during variable environmental conditions, and the subsequent conditional release of genetic variation under periods of environmental stasis (reviewed in Snell-Rood et al. 2010). For instance, in cases in which gene expression is restricted to a subset of alternative phenotypes or environments, and individuals experience only one such environment during their lifetime, gene copies residing in non-expressing individuals are not screened by selection. Any mutations that may reside in such copies are predicted to accumulate in a population in proportion to the frequency of individuals experiencing the non-inducing environment (VanDyken and Wade 2010). Studies on male-specific gene expression in

aphids (in which males are induced only every 10–20 generations; Brisson and Nuzhdin 2008) and maternal effect genes in *Drosophila* (Cruickshank and Wade 2008) support the prediction of mutations accumulating as a consequence of conditional gene expression. During periods of environmental stasis of inducing environments, the resulting accumulated variation could then be confronted with the full strength of selection, possibly enabling rapid evolutionary responses and adaptive divergences between populations. These predictions remain to be tested in natural populations (Snell-Rood et al. 2010).

Empirical support, especially from studies on insects, does exist for another form of developmental plasticity-mediated accumulation and release of genetic variation, namely under conditions of stress. Recall that developmental plasticity on some levels of biological organization often enables phenotypic constancy on others. Case in point is the facultative up-regulation of heat shock proteins in the face of temperature stress. Heat shock proteins act as chaperones and correct the 3-dimensional folding of proteins, which is increasingly prone to errors as temperatures become more stressful (Morimoto et al. 1997). In so doing, heat shock proteins may also act as buffers against genetic variants by corraling diverse genotypes to converge onto a single protein shape, that is, until the chaperoning capacity of heat shock proteins is exceeded, as might be the case during periods of prolonged stress or in response to sensitizing mutations. Laboratory studies on a diverse array of organisms between plants and fungi to animals, including insects, have highlighted the role of heat shock proteins and temperature stress as a means of accumulating and releasing selectable phenotypic diversity (Rutherford and Lindquist 1998; Queitsch et al. 2002; Cowen and Lindquist 2005; Suzuki and Nijhout 2006). In these studies, environmental stress resulted in a remarkable increase in the amount of selectable phenotypic variation, enabling rapid responses to artificial selection—including some reminiscent of naturally evolved phenotypes (Suzuki and Nijhout 2006). It is likely, though clearly in need of empirical confirmation, that many types of

developmentally plastic processes other than heat shock protein induction similarly function as capacitors for dormant genetic variation that may be released during periods of stress. What is entirely unclear, however, are the roles such accumulation and release may play in natural populations and naturally evolved responses to environmental variation, representing one of the most exciting current frontiers at the interface of evolutionary- and ecological-developmental biology.

#### 18.4.2 Developmental Plasticity, Evolvability, and the Differential Diversification of Arthropod Lineages

Are there reasons to believe that the contributions of developmental plasticity to evolvability highlighted above, which should be applicable to a wide range of organisms including arthropods, might have nevertheless disproportionately contributed to diversification and innovation of particular arthropod lineages? The answer is likely yes, though thorough comparisons akin to Yang's (2001) study introduced above are clearly needed to better understand this issue. For instance, it is very likely that the high levels of spatial and temporal modularity seen in certain arthropod taxa, such as the holometabolous insects, potentiated the degree to which developmental plasticity was able to facilitate subsequent diversification and innovation. For instance, developmental plasticity and spatial and temporal modularity frequently interact during insect development, enabling body-region and stage-specific diversification of conditional trait expression (see Fig. 18.3c for a spectacular example). Vivid examples of this can be seen during caste formation in social insects (e.g. Wheeler 1986, 1991; Emlen and Nijhout 2000) or the production of alternative male phenotypes (Emlen et al. 2005; Snell-Rood et al. 2011). In each case, facultative-, stage- and segment-specific modulation of development interact, allowing different body regions of the

same individual and stage to exhibit very different responses (from gene expression and growth allometries to pattern formation) to the same environmental changes (such as nutritional or seasonal conditions). This in turn has allowed taxa to diversify in the nature of body- and stage-specific responses, an evolutionary flexibility that likely contributed to the enormous diversity of social castes seen in the Hymenoptera or the diversification of alternative male morphologies observed in a wide range of insect orders (Emlen and Nijhout 2000).

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### 18.5 Final Remarks

In this chapter, we posited that arthropod evolvability was differentially enabled in different lineages through spatial modularity, ontogenetic modularity, developmental plasticity, and the interactions among them. Combined, this allowed segments, appendages, and their developmental responses to environmental changes to diversify in a stage-specific manner, thereby elevating diversification rates and facilitating the evolution of complex novel traits. Given the persistence and continued diversification of many arthropod lineages into present times, there is no reason to believe that this process is somehow over. Instead, many opportunities exist, now perhaps more than ever, to examine the interplay between ecology and development in enabling and shaping arthropod evolution in nature.

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### References

- Akam M (1989) Hox and HOM: homologous gene clusters in insects and vertebrates. *Cell* 57:347–349  
 Akam ME, Dawson I, Tear G (1988) Homeotic genes and the control of segment diversity. *Development* 104:123–133

- Angelini DR, Kaufman TC (2005a) Comparative developmental genetics and the evolution of arthropod body plans. *Annu Rev Genet* 39:95–119
- Angelini DR, Kaufman TC (2005b) Insect appendages and comparative ontogenetics. *Dev Biol* 286:57–77
- Averof M, Patel NH (1997) Crustacean appendage evolution associated with changes in Hox gene expression. *Nature* 388:682–686
- Bradshaw WE, Quebodeaux MC, Holzapfel CM (2003) Circadian rhythmicity and photoperiodism in the pitcher-plant mosquito: Adaptive response to the photic environment or correlated response to climatic adaptation? *Am Nat* 161:735–748
- Branham MA, Wenzel JW (2003) The origin of photic behavior and the evolution of sexual communication in fireflies (Coleoptera: Lampyridae). *Cladistics* 19:1–22
- Brisson JA, Nuzhdin SV (2008) Rarity of males in pea aphids results in mutational decay. *Science* 319:58
- Brusca RC, Brusca GJ (2002) *Invertebrates*. Sinauer, Sunderland
- Carroll SB, Gates J, Keys DN, Paddock SW, Panganiban GE, Selegue JE, Williams JA (1994) Pattern formation and eyespot determination in butterfly wings. *Science* 265:109–114
- Chapman RF (1998) *The insects: structure and function*. Cambridge University Press, Cambridge
- Cohen SM, Brönner G, Küttner F, Jürgens G, Jäckle H (1989) *Distal-less* encodes a homeodomain protein required for limb development in *Drosophila*. *Nature* 338:432–434
- Conway Morris S, Peel JS, Higgins AK, Soper NJ, Davis NC (1987) A Burgess Shale-like fauna from the Lower Cambrian of North Greenland. *Nature* 326:181–183
- Cowen LE, Lindquist S (2005) Hsp90 potentiates the rapid evolution of new traits: drug resistance in diverse fungi. *Science* 309:2185–2189
- Cruickshank T, Wade MJ (2008) Microevolutionary support for a developmental hourglass: gene expression patterns shape sequence variation and divergence in *Drosophila*. *Evol Dev* 10:583–590
- De Cock R, Matthysen E (1999) Aposematism and bioluminescence: experimental evidence from glow-worm larvae (Coleoptera: Lampyridae). *Evol Ecol* 13:619–639
- Denlinger DL (2002) Regulation of diapause. *Annu Rev Entomol* 47:93–122
- Emlen DJ, Hunt J, Simmons LW (2005) Evolution of sexual dimorphism and male dimorphism in the expression of beetle horns: phylogenetic evidence for modularity, evolutionary lability, and constraint. *Am Nat* 166:S42–S68
- Emlen DJ, Nijhout HF (2000) The development and evolution of exaggerated morphologies in insects. *Annu Rev Entomol* 45:661–708
- Force A, Lynch M, Pickett FB, Amores A, Yan YL, Postlethwait J (1999) Preservation of duplicate genes by complementary, degenerative mutations. *Genetics* 151:1531–1545
- Galis F, Metz JAJ (2007) Evolutionary novelties: the making and breaking of pleiotropic constraints. *Integr Comp Biol* 47:409–419
- Grimaldi DA, Engel MS (2005) *Evolution of the insects*. Cambridge University Press, New York
- Gullan PJ, Cranston PS (2004) *The insects: an outline of entomology*, 3rd edn. Wiley, London
- Halder G, Callaerts P, Gehring W (1995) Induction of ectopic eyes by targeted expression of the eyeless gene of *Drosophila*. *Science* 267:1788–1792
- Harvey EN, Hall RT (1929) Will the adult firefly luminesce if its larval organs are entirely removed? *Science* 69:253–254
- Heming BS (2003) *Insect development and evolution*. Cornell University Press, Ithaca
- Hess WN (1922) Origin and development of the light-organs of *Photuris pennsylvanica* de Geer. *J Morphol* 36:244–277
- Hou XG, Aldridge RJ, Bergström J, Siveter DJ, Feng XH (2004) The Cambrian fossils of Chengjiang, China. Blackwell Science, London
- Hughes CL, Kaufman TC (2002a) Hox genes and the evolution of the arthropod body plan. *Evol Dev* 4:459–499
- Hughes CL, Kaufman TC (2002b) Exploring the myriapod body plan: expression patterns of the ten Hox genes in a centipede. *Development* 129:1225–1238
- Kazunori Y (2012) The treehopper's helmet is not homologous with wings (Hemiptera: Membracidae). *Syst Entomol* 37:2–6
- Khadjeh S, Turetzek N, Pechmann M, Schwager EE, Wimmer EA, Damen WGM, Prpic NM (2012) Divergent role of the Hox gene *Antennapedia* in spiders is responsible for the convergent evolution of abdominal limb repression. *Proc Natl Acad Sci USA* 109:4921–4926
- Kijimoto T, Andrews J, Moczek AP (2010) Programmed cell death shapes the expression of horns within and between species of horned beetles. *Evol Dev* 12:449–458
- Koutsos AC, Blass C, Meister S, Schmidt S, MacCallum R, Soares MB, Collins FH, Benes V, Zdobnov E, Kafatos FC, Christophides GK (2007) Life cycle transcriptome of the malaria mosquito *Anopheles gambiae* and comparison with the fruitfly *Drosophila melanogaster*. *Proc Natl Acad Sci USA* 104:11304–11309
- Lewis DL, DeCamillis M, Bennett RL (2000) Distinct roles of the homeotic genes *Ubx* and *Abd-A* in beetle embryonic abdominal appendage development. *Proc Natl Acad Sci USA* 97:4504–4509
- Lewis EB (1978) A gene complex controlling segmentation in *Drosophila*. *Nature* 276:565–570
- Lloyd JE (1965) Aggressive mimicry in *Photuris*: firefly femmes fatales. *Science* 149:653–654
- Marinotti O, Calvo E, Nguyen QK, Dissanayake S, Ribeiro JMC, James AA (2006) Genome-wide analysis of gene expression in adult *Anopheles gambiae*. *Insect Mol Biol* 15:1–12

- Mente E (2008) Reproductive biology of crustaceans: case studies of decapod crustaceans. Science Publishers, Enfield
- Mikó I, Friedrich F, Yoder MJ, Hines HM, Deitz LL, Bertone MA, Selmann KC, Wallace MS, Deans AR (2012) On dorsal prothoracic appendages in treehoppers (Hemiptera: Membracidae) and the nature of morphological evidence. *PLoS ONE* 7(1):e30137. doi:10.1371/journal.pone.0030137
- Minelli A (2003) The development of animal form: ontogeny, morphology and evolution. Cambridge University Press, Cambridge
- Minelli A (2009) Perspectives in animal phylogeny and evolution. Oxford University Press, Oxford
- Minelli A, Brena C, Deflorian G, Maruzzo D, Fusco G (2006) From embryo to adult—beyond the conventional periodization of arthropod development. *Dev Genes Evol* 216:373–383
- Moczek AP (2006) Pupal remodeling and the development and evolution of sexual dimorphism in horned beetles. *Am Nat* 168:711–729
- Moczek AP (2010) Phenotypic plasticity and diversity in insects. In: Minelli A, Fusco G (eds) From polyphenism to complex metazoan life cycles, philosophical transactions of the royal society B vol 365. Royal Society of publishing, London, pp 593–603
- Moczek AP, Cruickshank TE, Shelby JA (2006) When ontogeny reveals what phylogeny hides: gain and loss of horns during development and evolution of horned beetles. *Evolution* 60:2329–2341
- Moczek AP, Nagy LM (2005) Diverse developmental mechanisms contribute to different levels of diversity in horned beetles. *Evol Dev* 7:175–185
- Moczek AP, Nijhout HF (2002) Developmental mechanisms of threshold evolution in a polyphenic beetle. *Evol Dev* 4:252–264
- Moczek AP, Rose DJ (2009) Differential recruitment of limb patterning genes during development and diversification of beetle horns. *Proc Natl Acad Sci USA* 106:8992–8997
- Moczek AP, Sultan S, Foster S, Ledon-Rettig C, Dworkin I, Nijhout HF, Abouheif E, Pfennig D (2011) The role of developmental plasticity in evolutionary innovation. *Proc R Soc B* 278:2705–2713
- Morata G (2001) How *Drosophila* appendages develop. *Nat Rev Mol Cell Biol* 2:89–97
- Morimoto RI, Kline MP, Bimston DN, Cotto JJ (1997) The heat-shock response: regulation and function of heat-shock proteins and molecular chaperones. *Essays Biochem* 32:17–29
- Nijhout HF (1994) Insect hormones. Princeton University Press, Princeton
- Nijhout HF (1999a) Hormonal control in larval development and evolution—insects. In: Hall BK, Wake MH (eds) The origin and evolution of larval forms. Academic, San Diego, pp 218–254
- Nijhout HF (1999b) Control mechanisms of polyphenic development in insects. *Bioscience* 49:181–192
- Nijhout HF (2003) Development and evolution of adaptive polyphenisms. *Evol Dev* 5:9–18
- Nijhout HF (2013) Arthropod developmental endocrinology. In: Minelli A, Boxshall G, Fusco G (eds) Arthropod biology and evolution. Springer-Verlag Berlin Heidelberg
- Ødegaard F (2000) How many species of arthropods? Erwin's estimate revised. *Biol J Linn Soc* 71:583–597
- Ohno S (1970) Evolution by gene duplication. Springer, Berlin
- Panganiban G, Irvine SM, Lowe C, Roehl H, Corley LS, Sherbon B, Grenier JK, Fallon JF, Kimble J, Walker M, Wray GA, Swalla BJ, Martindale MQ, Carroll SB (1997) The origins and evolution of animal appendages. *Proc Natl Acad Sci USA* 94:5162–5166
- Pfennig DW, McGee M (2010) Resource polyphenism increases species richness: a test of the hypothesis. *Phil Trans R Soc B* 365:577–591
- Pfennig D, Wund MA, Snell-Rood EC, Cruickshank T, Schlichting CD, Moczek AP (2010) Phenotypic plasticity's impacts on diversification and speciation. *Trends Ecol Evol* 25:459–467
- Prud'homme B, Minervino C, Hocine M, Cande JD, Aouane A, Dufour HD, Kassner VA, Gompel N (2011) Body plan innovation in treehoppers through the evolution of an extra wing-like appendage. *Nature* 473:83–86
- Queitsch C, Sangster TA, Lindquist S (2002) Hsp90 as a capacitor of phenotypic variation. *Nature* 417:618–624
- Rabossi A, Acion L, Quesada-Allue LA (2000) Metamorphosis-associated proteolysis in *Ceratitis capitata*. *Entomol Exp Appl* 94:57–65
- Regier JC, Shultz JW, Zwick A, Hussey A, Ball B, Wetzer R, Martin JW, Cunningham CW (2010) Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences. *Nature* 463:1079–1082
- Rutherford SL, Lindquist S (1998) Hsp90 as a capacitor for morphological evolution. *Nature* 396:336–342
- Scharloo W (1991) Canalization: genetic and developmental aspects. *Ann Rev Ecol Syst* 22:65–93
- Schlichting CD, Pigliucci M (1995) Gene regulation, quantitative genetics, and the evolution of reaction norms. *Evol Ecol* 9:154–168
- Schlichting CD, Pigliucci M (1998) Phenotypic evolution: a reaction norm perspective. Sinauer, Sunderland
- Scholz G (2004) On comparisons and causes in evolutionary developmental biology. In: Minelli A, Fusco G (eds) Evolving pathways: key themes in evolutionary developmental biology. Cambridge University Press, Cambridge, pp 144–159
- Scoville A, Pfrender M (2010) Phenotypic plasticity facilitates recurrent rapid adaptation to introduced predators. *Proc Natl Acad Sci USA* 107:4260–4263
- Snell-Rood EC, Cash A, Han MV, Kijimoto T, Andrews J, Moczek AP (2011) Developmental decoupling of alternative phenotypes: insights from the transcriptomes of horn-polyphenic beetles. *Evolution* 65:231–245

- Snell-Rood EC, Papaj DR (2009) Patterns of phenotypic plasticity in common and rare environments: a study of host use and color learning in the cabbage white butterfly, *Pieris rapae*. *Am Nat* 173:615–631
- Snell-Rood EC, VanDyken JD, Cruickshank TE, Wade MJ, Moczek AP (2010) Toward a population genetic framework of developmental evolution: costs, limits, and consequences of phenotypic plasticity. *Bio Essays* 32:71–81
- Storch V, Welch U (1991) *Systematische zoologie*. Gustav Fischer Verlag, Stuttgart
- Suzuki Y, Nijhout HF (2006) Evolution of a polyphenism by genetic accommodation. *Science* 311:650–652
- Tauber MJ, Tauber CA (1972) Geographic variation in critical photoperiod and in diapause intensity of *Chrysopa carnea* (Neuroptera). *J Ins Physiol* 18:25–29
- Truman JW, Riddiford LM (2002) Endocrine insights into the evolution of metamorphosis in insects. *Annu Rev Entomol* 47:467–500
- Vachon G, Cohen B, Pfeifle C, McGuffin ME, Botas J, Cohen SM (1992) Homeotic genes of the Bithorax complex repress limb development in the abdomen of the *Drosophila* embryo through the target gene *Distal-less*. *Cell* 71:437–450
- Valentine JW (2004) *On the origin of phyla*. University of Chicago Press, Chicago
- Van Dyken JD, Wade MJ (2010) Quantifying the evolutionary consequences of conditional gene expression in time and space. *Genetics* 184:439–453
- Warren RW, Nagy L, Selegue J, Gates J, Carroll S (1994) Evolution of homeotic gene-regulation and function in flies and butterflies. *Nature* 372:458–461
- Wasik BR, Rose DJ, Moczek AP (2010) Beetle horns are regulated by the Hox gene, *Sex combs reduced*, in a species- and sex-specific manner. *Evol Dev* 12:353–362
- West-Eberhard MJ (2003) *Developmental plasticity and evolution*. Oxford University Press, New York
- Wheeler DE (1986) Developmental and physiological determinants of caste in social Hymenoptera: evolutionary implications. *Am Nat* 128:13–34
- Wheeler DE (1991) Developmental basis of worker caste polymorphism in ants. *Am Nat* 138:1218–1238
- Wheeler DE, Nijhout HF (2003) A perspective for understanding the modes of juvenile hormone action as a lipid signaling system. *Bio Essays* 25:994–1001
- Whitman DW, Ananthakrishnan TN (2009) *Phenotypic plasticity of insects: mechanisms and consequences*. Science Publishers, Enfield
- Yang AS (2001) Modularity, evolvability, and adaptive radiations: a comparison of the hemi- and holometabolous insects. *Evol Dev* 2:59–72