

Review

Developmental plasticity and the evolution of animal complex life cycles

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Metazoan life cycles can be complex in different ways. A number of diverse phenotypes and reproductive events can sequentially occur along the cycle, and at certain stages a variety of developmental and reproductive options can be available to the animal, the choice among which depends on a combination of organismal and environmental conditions.

We hypothesize that a diversity of phenotypes arranged in developmental sequence throughout an animal's life cycle may have evolved by genetic assimilation of alternative phenotypes originally triggered by environmental cues.

This is supported by similarities between the developmental mechanisms mediating phenotype change and alternative phenotype determination during ontogeny and the common ecological condition that favour both forms of phenotypic variation.

The comparison of transcription profiles from different developmental stages throughout a complex life cycle with those from alternative phenotypes in closely related polyphenic animals is expected to offer critical evidence upon which to evaluate our hypothesis.

Keywords: comparative analysis; larvae; life cycle evolution; metamorphosis; polyphenism

1. WHAT IS A COMPLEX LIFE CYCLE?

There is no single best definition of a complex life cycle. Complexity, in general and also specifically in biology, is an intuitively appealing concept, which can be defined and applied in many, possibly in too many different ways. Thus, in each instance, we must specify the perspective from which we are considering our objects of study, and thus the kind of comparison from which differences in complexity can be evaluated and discussed (e.g. Saunders & Ho 1984; Bonner 1988; McShea 1991, 1992, 1996*a,b*, 2000; Bell & Mooers 1997; Fusco & Minelli 2000). However, if complexity defies straight, uncontroversial definition, the same must be said of an animal's life cycle.

Problems in circumscribing a life cycle are twofold. First, fixing the point of origin of a cycle is often subjective, although the periodization of animal development is most frequently presented by fixing fertilization as its starting point, but the onset of zygotic gene expression could be suggested as a reasonable alternative, and still other choices could be made by developmental biologists (and bioethicists). This translates into a problem of 'alignment of ontogenies' for comparative purposes. Second, and more relevant to this article's focus, is that the life cycles of several metazoans depart so much from the conventional egg-to-adult sequence of stages that even the number

of generations to be recognized within one cycle is sometimes open to dispute. Facing these difficulties should not be the cause for despair. Indeed, the diversity of life cycles and the different degrees to which specific developmental stages or events can be distinguished may turn out to be a legitimate and profitable subject of investigation from an evolutionary point of view.

We start with a short discussion of the criteria adopted to dissect the course of development into meaningful and manageable temporal segments (periodization). Then, we consider a selection of life cycles that put into question the legitimacy of presenting the conventional egg-to-adult-to-egg (or adult-to-egg-to-adult) life cycle as a general term of reference for studying the evolution of development.

Next, we briefly discuss why we should relax the usual alternative between spatial and temporal aspects of patterning and differentiation. This provides a scenario against which we introduce our hypothesis that alternative phenotypes originally produced under the effect of external cues (polyphenism) may have provided the source for the evolution of sequentially arranged phenotypes of a life cycle. This course of evolution could have happened in so far as the conditions leading to the release of a particular phenotype, rather than to other phenotypes compatible with the same genotype, would have become increasingly internalized, thus turning those phenotypes from alternatives within a polyphenic space into strictly predictable sequential stages in a progressively more complex life cycle.

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2. DESCRIBING ONTOGENIES: PERIODIZATION AND DEVELOPMENTAL COMPLEXITY

A life cycle does not always coincide with an individual's ontogeny. Life cycles with an alternation of generations are the rule in mosses, ferns and flowering plants, but comparable conditions are found in metazoan life cycles as well. Reproductive events separating distinct generations can punctuate a *multi-generation life cycle*. Two well-known examples are the regular alternation between sexual and asexual generations within one life cycle (metagenesis), as in many cnidarians, and the regular alternation between amphigonic and parthenogenic generations (heterogony) found, for example, in many aphids, monogonont rotifers and cladoceran crustaceans. But also regular seasonal polyphenism (see below) might be described as multi-generation life cycle.

The description of an animal's development is a historical narrative, an exercise we cannot easily accomplish without adopting a scheme for the temporal distribution of events, that is, a *periodization*.

Embryonic versus post-embryonic, or larval versus adult, are the most obvious examples of periodization of animal development. The standard tables established by embryologists for a few more intensively studied species are examples of more detailed, but not necessarily less arbitrary periodizations (Love 2010). In all these efforts, partitioning an animal's life into temporal segments means focusing on one or a few of the most conspicuous developmental processes, or events, at the same time disregarding other processes, or events, that would suggest a different periodization.

This is most conspicuous in analysing the post-embryonic development of arthropods, where all current descriptions are essentially based on a 'cuticular view' of developmental events (Minelli *et al.* 2006). The sequence of moults is the most general criterion we use when, for instance, in a trilobite's development we distinguish among the different meraspid 'degrees', or between meraspid and holaspid periods (e.g. Hughes *et al.* 2006). The same criterion is applied when we separate an orthonauplius from a metanauplius, or a nauplius from a copepodite in the life cycle of a crustacean (e.g. Ferrari & Dahms 2007). However, there are many important events in the development of internal organs which are not punctuated by moults, and whose consideration could suggest a different periodization.

In a sense, within an animal's ontogeny many different, intertwining processes go on, and their occasional matching in time should not induce us to regard those events as the precise starting point of a significant segment of ontogeny. Caution should extend even to apparently conspicuous events such as an arthropod's hatching—an event that does not closely match in a generalized, predictable way with the animal's progression from the helpless condition of immobile embryo to that of an active, self-sufficient larva or juvenile (Minelli *et al.* 2006).

3. LINEAR DEVELOPMENTAL COMPLEXITY

However defined and eventually measured, developmental complexity is a function of the number and

magnitude of changes an animal undergoes throughout its life cycle: changes in form, as between the pluteus larva and the adult sea urchin; changes in environmental conditions, or lifestyle, as between the pelagic larva and the benthic adult of many marine invertebrates; but also changes in reproductive modes, when more reproductive phases are part of the same multi-generational life cycle, as in the case of cnidarians. Moreover, there are species, developmental stages or environmental conditions in which more than one option for change (either in form, environmental requirements or reproductive mode) is open to the animal, and therefore, stages that can be reached through different (convergent) processes of change or different reproductive modes.

Before considering these developmental switches, and the examples where nearly identical phenotypes are obtained by different individuals of the same species following different developmental routes, let us consider the diversity of forms, developmental changes and reproductive modes that may fit together in the life cycle of a given metazoan species. These can be considered as descriptors of the 'linear complexity' of their respective life cycles.

Aspects to be considered are the number of different phenotypes we can distinguish throughout the development of a metazoan species, and the degree of morphological differences among them. Restricting our view to the post-embryonic segment of the life cycle, there are virtually all possible degrees of complexity between the apparently uneventful growth to maturity of a newly hatched earthworm, leech, snail or lizard, and the dramatic contrast between a pilidium, a trochophore or a tornaria and the corresponding adults of nemertean, polychaetes and enteropneusts. In all these examples, the intervening segment of life cycle during which metamorphosis occurs has generally not been singled out by zoologists as a well circumscribed stage worthy of independent recognition and name, while this has been done for holometabolous insects, where a pupa is distinguished between the larva and adult, even in those examples where the structural changes at metamorphosis are much less dramatic than in the case of a pilidium turning into a juvenile nemertean, or a bipinnaria turning into a young sea star. To be sure, the almost 'frozen' external morphology of arthropods between two consecutive moults and the more or less complete immobility of the pupa, as opposed to the active life of both mature larva and adult of the nemertean and sea star, allows a more detailed periodization of development, and this may suggest, perhaps unduly, a higher degree of developmental complexity.

With all the obvious contrasts between larval and adult organization, nemertean, echinoderm and holometabolous insects are far from representing the highest degrees of linear developmental complexity. The number of structurally different phenotypes throughout a developmental history is distinctly higher in other metazoans, such as in hypermetabolous insects, rhizocephalan crustaceans and digenean flatworms. All three groups are representative of different aspects of the matter.

From their hatching from the egg to the time they turn into pupae, hypermetabolous insects develop through several larval instars with distinctly different organization. For example, in the blister beetles (Coleoptera: Meloidae), the unfeeding and often phoretic first larval instar (the triungulin), provided with long walking legs, changes into a feeding, sedentary second-instar larva with extremely reduced legs; a few more instars follow, including a resting pupa-like coarctate stage, which eventually moults to a further active larva, followed by the real pupa and adult (e.g. Bologna & Pinto 2001; Heming 2003; Bologna *et al.* 2008). Comparison with the developmental schedules of species in closely related beetle families with ordinary holometabolous life cycles suggests that the morphologically most conspicuous developmental novelty evolved in Meloidae is the long-legged first-instar larva, whereas the subsequent stages represent a more conservative model. We will return later to the evolutionarily frequent occurrence of novelties affecting early post-embryonic stages.

Among rhizocephalan crustaceans, the rich palette of post-embryonic developmental stages includes nauplius and cypris larvae comparable to those of other crustaceans such as the barnacles, and the profoundly modified, parasitic fertile stages. The dramatic changes from the conventional, free-living larva to the uniquely modified, parasitic adult are released at the moment the larva settles on its future host. The larva abandons its cuticle, turning into a kind of amoeboid infective stage, in some species fragmenting into smaller units. In *Loxothylacus panopaei*, a parasite of crabs, the infective stage apparently dissociates into single cells, each of which is probably able to develop into a female adult (Glennner & Høeg 1995). If this extraordinary observation is confirmed, this will represent a new, idiosyncratic example of what is currently known as metagenesis. A parallel breakdown of a conventional life cycle originally involving sexual reproduction and indirect development through larval stages and metamorphosis has been recorded for a bivalve mollusc, that is, for a representative of a phylum where, similar to arthropods, we are not expecting metagenesis to occur. The molluscan example is provided by the freshwater mussel *Mutela bourguignati*. Its haustorial larva, which is a fish parasite, produces a bud that eventually turns into a juvenile mussel (Fryer 1961).

One might object, in the last example especially, to the suggested interpretation of these life cycles as involving an alternation of generations. If (when) only one sexual adult is produced, the fact that only a part of the larva (the bud) actually contributes to producing the adult is not that different from the events accompanying the metamorphosis of a nemertean, or a fly, where only a limited portion of the larval organs and tissues contributes to the adult's body. This argument is based on a distinction between development and reproduction that rests on a 'demographic' principle: development changes an individual A into A_1 , whereas reproduction changes A into $A + A_1$ or $(A+)A_1 + \dots A_n$. If the larva produces only one bud, thus only one adult, this would be regarded as an instance of metamorphosis, but if

the larva produces more than one bud, this would be easily labelled as a reproductive event, more likely, as an example of asexual reproduction corresponding, specifically, to the asexual phase in a metagenetic cycle (Minelli 2009). However, on the basis of the biological processes involved, the two cases are not that different, notwithstanding their 'significance'. These examples show how the categories into which we ordinarily shoehorn metazoan life cycles and their component phases and events can turn out to be inadequate to investigate the evolution of animal life cycles' diversity.

In some metazoan groups, knowledge is so incomplete that any interpretation or classification can be but tentative. This is true of the flukes (digeneans). The life cycle of these parasitic flatworms is usually described as including a regular alternation between a generation of hermaphroditic maritae producing fertilized eggs and a generation (more often, a sequence of two or more generations) of parthenitae that are usually regarded as reproducing through unfertilized eggs. However, whether the parthenitae actually reproduce by parthenogenesis, or otherwise, is still far from clear, and there is no reason to expect that all species and 'generations' will behave the same way. In some families (Fasciolidae and Transversotrematidae), each miracidium, i.e. the larva that issued from the fertilized egg produced by the marita, may give rise to two parthenitae (Galaktionov & Dobrovolskij 2003). This is an example of reproduction at a somatically larval stage, and zoologists would call this an instance of progenesis. However, as said, a fundamental question remains: what is the nature of the cells from which the 'embryos' (or internal buds?) actually develop. Many other examples of the diversity of digenean life cycles can be found in Galaktionov & Dobrovolskij (2003).

4. DEVELOPMENTAL SWITCHES

Besides the universal occurrence of linear developmental complexity, such as the conspicuous examples summarized above, many metazoan life cycles include a further dimension of complexity in the form of a plethora of alternative phenotypes to which development may give rise, subsequent to receiving from the environment a diversity of physical, chemical or biological stimuli to be processed in conformity to genetically inherited reaction norms.

Several examples of this polyphenism are well known (see West-Eberhard 2003), where the long-term effect of these externally induced developmental switches is the appearance of morphologically and physiologically distinct adult phenotypes such as the solitary and gregarious phases of some locusts and—rare exceptions excluded—the castes of social insects. From external stimuli, acting on the developing animal at a critically sensitive phase, periodically alternating phenotypes arise, such as the dry season versus wet season phenotypes of some butterflies (e.g. the European nymphalid *Araschnia levana* and the African satyrid *Bicyclus* spp.), or the different morphs prevailing in successive generations of some freshwater cladocerans of the genus *Daphnia*.

In some species of soil nematodes, adverse environmental conditions trigger post-embryonic development towards the production of a so-called dauer larva, which is able to survive long periods of starvation, as an alternative to a normal third-instar larva (Cassada & Russell 1975). In other nematodes, larvae equivalent to the dauer larvae of free-living species have turned into infesting parasitic instars (Anderson 1984; Poulin 2007). The flexible boundary between non-parasitic and parasitic lifestyle is well exemplified by another nematode, *Strongyloides ratti*, which can develop either 'directly' by producing larvae that infect new hosts, or 'indirectly', with a generation of infective larvae alternating with one or more fully free-living generations (Fenton *et al.* 2004).

Alternative options can characterize the different modes of sequential hermaphroditism within the same species. In several species of tanaid crustaceans, the environmental control of sex is unusually complex and inadequately understood. In these animals, there are many alternative ways to become a male. In some representatives of the suborder Tanaidomorpha, at least three different developmental routes may coexist within one species, with primary males developing from male juveniles, whereas secondary and tertiary males are proterogynous hermaphrodites that have previously produced, respectively, one or two broods as females (Larsen 2005). Females and primary, secondary and tertiary males differ so profoundly in morphology, that conspecific males of the different classes have often been assigned to different species (correct assignment of conspecific females is often impossible without direct evidence from observed mating, moulting or cohabitation in a female's home tube; Sieg 1978; Larsen 2001). Additional options are available to some tanaid species, including the development of primary males from either a juvenile I or an earlier stage of manca II as in *Apseudes heroae* (Schmidt *et al.* 2002).

It is elementary textbook knowledge that environmentally induced switches extend beyond morphology, to encompass also an animal's reproductive mode. In some insects, such as the beetle *Micromalthus debilis* (Pollock & Normark 2002) and several species of heteropezine midges (Nikolei 1961; Wyatt 1961, 1964), largely unknown external cues induce a larva to complete metamorphosis into a conventional adult, or to become a progenetic (paedogenetic) producer of mature eggs and/or larvae of either one or both sex.

5. ALTERNATIVE DEVELOPMENTAL ROUTES TO EQUIVALENT PHENOTYPES

If a complex life cycle presents a number of alternative phenotypes (through divergent developmental pathways), this implies that at some point, distinct alternative developmental routes must converge towards the same phenotype. For example, tunicates such as the colonial sea squirts (*Botryllus* spp.) can reproduce both sexually, through egg fertilization followed by embryonic and larval development, and asexually, from a bud, and without intervening larvae: the full-grown animals are nevertheless very similar in gross anatomy and in many details of structure (Manni & Burighel 2006).

In other metazoans, alternative forms of larvae or juveniles eventually give rise to identical adults. This phenomenon of developmental plasticity, known as poecilogony (Giard 1905), has been recorded from insects, nematodes, polychaetes, opisthobranch gastropods and amphibians (Begun & Collins 1992; Greene 1999). In some spionid polychaetes, both planktotrophic and lecithotrophic larvae may occur in a single species (Larink & Westheide 2006), and in the marine gastropod *Haminaea callidegenita*, both veliger larvae and 'post-larval' juveniles are produced from the same egg mass (Gibson & Chia 1989; Chia *et al.* 1996). In another marine gastropod, *Alderia modesta*, the siblings are sometimes all planktotrophic, or all lecithotrophic, but sometimes both (Krug 1998).

6. THE ORIGINS OF COMPLEX LIFE CYCLES

(a) *Recapitulation versus intercalation*

Traditional interpretations of the origin and evolution of complex life cycles have been dominated by two contrasting scenarios, the *recapitulationist* and the *intercalary*, traditionally associated with the names of Ernst Haeckel and Walter Garstang, respectively. An extensive literature, of which we will mention only the classic work of Gould (1977) and the more recent analyses of Hall (1998) and Minelli (2009), has demonstrated how inadequately either hypothesis represents the diversity of evolutionary changes in the ontogenies of different metazoan lineages, and also how much the cited authors, Haeckel especially, owed to earlier authors, including some pre-Darwinians. However, despite this general agreement on the historical perspective to be adopted in evaluating Haeckel's (1866) and Garstang's (1922) contributions to understanding life cycle evolution, and also on the inapplicability of either scenario to a great number of actual examples, it is not commonly realized that neither scenario offers more than a generalized and hypothetical description of developmental sequences. Similar to another fashionable concept, heterochrony (see Raff & Wray 1989; McKinney & McNamara 1991; McNamara 1995; Hall 1998; Minelli 2003), recapitulation and intercalation describe specific (and generally interesting, so far as confirmed) patterns of change that ask for mechanistic explanation.

Compared with the old scenarios of developmental evolution suggested by Haeckel and Garstang, it is more profitable to consider developmental instars and metamorphoses in terms of their adaptive value. Spending weeks in the plankton or metamorphosing into a benthic juvenile within hours since fertilization is clearly a choice on which natural selection has left its footprint in many marine invertebrates. Living within the soft cuticle of a freshly moulted arthropod is a vulnerable condition with which crabs have to cope many times during their growth, particularly when they are still young. But realizing that an animal is often subject to stronger selection during its early post-embryonic development than as an adult is not enough if we want to understand the evolution of developmental schedules. We must also know how selectable variation is distributed throughout an animal's development. This may seem an odd

question, as the animal's genome obviously does not change during its life, but we must consider that the phenotype, or the palette of phenotypes, an animal may express in a particular phase of its development is not necessarily the same as it can offer in other phases. This is particularly true if the animal is prone, in a specified developmental phase, to respond to unpredictable environmental cues by expressing a diversity of alternative phenotypes, i.e. if it exhibits polyphenism. The interpretation of metazoan life cycle evolution we are presenting in this paper rests specifically on this potential availability of phenotypic variation in some environmentally sensitive phases of development.

It is of interest that both the switch between alternative developmental routes and the developmental transitions involving major morphological and ecological changes often co-occur within the developmental schedule. We have seen such a coincidence between the phase at which some normal nematode larvae switch to a dauer fate, and the phase during which a free-living larva of other nematodes becomes parasitic. We will return to this example, as the gross parallelism between the normal to dauer and free living to parasite transitions is supported by mechanisms involving the same classes of molecules.

In holometabolous insects, the organization of the adult is generally more conservative than that of the larva (Minelli *et al.* 2006). The origin of the holometabolous condition is likely to be found in a previously fleeting pronymphal or prolarval stage corresponding to the last, still inactive pre-hatching stage (in some cases, an equally inactive hatchling) of hemimetabolous insects (Berlese 1913; Truman & Riddiford 1999). Adult polyphenism is frequent in insects, but is unlikely to influence the evolution of more complex life cycles, because, in all extant pterygote insects except mayflies, the adult ceases to moult. Thus, its form is frozen for its remaining life, be this in a basically invariant species-specific shape, or in one of the conspicuously distinct phenotypes, as in winged versus wingless aphids (Brisson 2010) or in male scarabs with shorter or longer horns (Moczek 2010). However, adult polyphenism is possibly more widespread in insects than these well-known examples would suggest. Indeed, differences between adult morphs are sometimes behavioural and physiological rather than morphological. Solitary and gregarious locusts are not dramatically different in size or shape. Still less conspicuous (but probably important in terms of adaptation) are the differences between two environmentally induced morphs in the seed beetle *Callosobruchus subinnotatus*, of which one is sedentary, the other adapted for dispersal (Appleby & Credland 2007).

(b) *From polyphenism to cell differentiation*

Whenever two or more alternative phenotypes produced by the developmental processing of different external cues turn out to have adaptive value, we can expect that in the long run their expression will become progressively less dependent on the environment, and more directly controlled by genes (genetic assimilation) (Schlichting & Pigliucci 1998; Moczek

2007). In the pea aphid *Acyrtosiphon pisum* (Brisson 2010), males are either winged or wingless, depending on a genetic polymorphism (Braendle *et al.* 2005a), but the gene locus (*aphicarus*) affecting male wing type is also involved in the polyphenic response to varying environmental cues that causes presence versus absence of wings in the females (Braendle *et al.* 2005b).

The hypothesis that a former polyphenism may have been 'internalized' in the course of evolution, resulting in the coexistence of alternative genetically controlled phenotypes as parts of a system of predictable complexity, was first suggested long ago (e.g. Zakhvatkin 1949).

The diverse cell types in a multicellular organism share (with a few marginal exceptions) an identical genome and their different phenotypes are largely the result of the history of their interactions with their proximate cellular environment. Thus, cell differentiation emerges from these studies as nothing else than a predictable and functional form of polyphenism.

This circumstance has suggested (Zakhvatkin 1949; Schlichting 2003; Valentine 2004; Mikhailov *et al.* 2009) that a first degree of cell differentiation within a multicellular organism may have originated by the stabilization, and increased predictability, of a pattern of coexistence of alternative cell phenotypes. Thus, what at an earlier stage of evolution might have been different forms within the polyphenism of an ancient eukaryote with unicellular organization may have evolved into the basis for cell differentiation within its multicellular descendants. This model could explain the origin of multicellulars with a small number of coexisting cell types, but this in turn may have facilitated the evolution of higher degrees of cell differentiation.

(c) *From polyphenism to developmental sequence*

The essence of Zakhvatkin's model is that the internalization of cues inducing the expression of what originally were alternative phenotypes of a polyphenic unicellular may have given rise to an orderly and predictable coexistence of these phenotypes in a precise spatial array. In this paper, we suggest that from the same beginnings (a polyphenism) a temporally (rather than spatially) consistent, predictable array of phenotypes in the form of structurally distinct stages within a complex life cycle may have evolved.

To give structure to a spatial array of cells or organs may not be much different from giving structure to a temporal sequence of stages (Minelli 2003). In this context, Kenyon *et al.* (1997) floated the interesting hypothesis that the early metazoans may have equally set up their *Hox* gene expression pattern either through the expression patterns of other genes that could provide cells with positional information, or through a tight temporal control of the *Hox* gene expression itself. Also, the variable expression of hermaphroditism, with sequential and simultaneous hermaphroditism, respectively, provides examples of temporal and spatial distribution of corresponding kinds of modules.

At least for mechanistically simple, though phenotypically conspicuous features such as the body colour of caterpillars, there is circumstantial evidence suggesting that a polyphenic trait can easily translate into a genetically controlled sequence of dramatically different phenotypes. In moths such as *Biston betularia*, the body colour of caterpillars matches closely the brown or green colour of the twigs of the host plant. In this species, the most important external cue triggering the realization of a given phenotype is the visual experience of the caterpillar, which has a much stronger effect than diet (Noor *et al.* 2008). In other lepidopterans there is a fixed developmental change in the colour of the larva, as in the swallowtail *Papilio xuthus*, where caterpillars in the fourth instar have a colour and dorsal tubercles through which they mimic bird droppings, while in the fifth and final instar they are smooth and green. In this species, these differences correlate with differential gene expression (Futahashi & Fujiwara 2008) that has become independent of external cues.

The more the expression of a specific phenotype falls under genetic control, the more it is likely to be expressed. In turn, its expression is likely to facilitate also the expression of other specific phenotypes in conserved developmental sequence. In this way, a series of different, sequentially realized alternative phenotypes compatible with the animal's genome, but individually expressed in the presence of different transcription patterns (see below), will gradually evolve towards a strictly controlled temporal sequence of developmental stages.

Also, the probability that this sequence will occasionally reverse will probably vanish soon, as demonstrated by the life cycles of most animal species. Exceptions to this rule are indeed extremely rare. Best known is the case of the hydrozoan *Turritopsis nutricula*, where a medusa, under certain conditions, is able to revert to a polyp (Bavestrello *et al.* 1992; Piraino *et al.* 1996). A less well investigated example is provided by the cercariae and metacercariae of some gymnophalline digeneans that do not transform, as expected, into adult maritae but revert instead to germinal sacs similar to those from which they were earlier produced (Galaktionov & Dobrovolskij 2003).

(d) *Conserved mechanisms*

If an animal's complex life cycle derives from diachronic fixation of the alternative phenotypes originally expressed as polyphenisms, this historical continuity is likely to have left an imprint in the internal mechanisms that mediate the most conspicuous developmental changes, as at metamorphosis. This is what is observed in insects, where 20-hydroxyecdysone and juvenile hormone, the principal hormones controlling moulting and metamorphosis, are also the principal mediators of polyphenic responses to external cues (Nijhout 1994, 1999, 2003).

Corresponding similarities have been discovered in nematodes. The physiological mechanism inducing the switch from normal to dauer larva has much in common with the mechanism by which an earlier, free-living stage turns into a more advanced parasitic

stage in other nematodes (Ogawa *et al.* 2009). In *Caenorhabditis elegans*, stressful conditions such as overcrowding, high temperature or starvation translate into pheromonal cues eventually processed through signalling pathways including insulin/IGF, TGF β -like and guanylyl cyclase pathways. As a result, the concentration of peculiar steroidal hormones (Δ 4-dafachronic acids and Δ 7-dafachronic acids) decreases, and the transition to dauer larva is released (Antebi *et al.* 1998, 2000; Snow & Larsen 2000; Motola *et al.* 2006; Giroux & Corey 2007). These hormones are required for dauer larva development in *C. elegans* (Vowels & Thomas 1992). But a form of dafachronic acid also has a role in the control of infectivity in parasites, as its application to infective larvae of the mammalian parasite *Strongyloides papillosus* transforms them into free-living worms.

(e) *Conserved environmental cues*

The fact that many dramatic events in metamorphosis are released by the contact of a parasite with its host suggests a genetically fixed (canalized) reaction norm that may have originated as an adaptively neutral, morphogenetic effect resulting from exposure to an external cue of the kind still provided by contact with the host.

We can expect that even after genetic fixation of a developmental switch, its expression may still depend on the availability of generic cues. This is what is found in many embryonic and post-embryonic developmental sequences, when examining conspecific larvae exposed to different environmental cues, or through comparisons of the larvae of closely related species. Environmental cues eliciting benthic settlement and metamorphosis in marine molluscan larvae are as varied as the species that respond to them (Jackson *et al.* 2002) and include chemicals released from rock-covering biofilms of bacteria and microalgae (Taylor *et al.* 1998), detritus (Stoner *et al.* 1996) and diverse molecules produced by benthic algae and other animals (Hadfield & Pennington 1990). There are also species that settle on the sea bottom and metamorphose in the absence of any apparent cue (Pechenik & Eyster 1989; Inestrosa *et al.* 1993). This parallels the lack of specificity often found in the cues provided by the intracellular and intercellular environment to embryos facing important developmental switches. For example, the embryos of two ascidians, *Halocynthia* and *Ciona* spp., share very similar early cell lineages, and a similar global logic of induction, but the specification of the secondary notochord cell lineage is induced by different molecules in the two animals (Lemaire 2009). A similar generic character in inducing cues has been found for vulva development in nematodes (Félix 2005).

(f) *Shared ecological context*

Another prediction we can derive from the hypothesis presented in this paper is that life cycle complexification is likely to originate, preferentially, in a less predictable and less stable, perhaps seasonally changing environment. This is the context where the extensive variation in external conditions is likely to

release extensive polyphenic responses. The alternative developmental sequences thus set in motion can occasionally turn out as 'natural capacitors for cryptic genetic variation' (Moczek 2007, p. 301; see also Rutherford & Lindquist 1998; Queitsch *et al.* 2002; Cowen & Lindquist 2005; Dworkin 2005a,b; Nijhout *et al.* 2006; Suzuki & Nijhout 2006).

Jacobs *et al.* (2008) have remarked that metamorphosis of the planktonic larvae of a great many marine invertebrate is both a developmental and an ecological transition (Hadfield *et al.* 2001; Jackson *et al.* 2002). This coincidence, irrespective of its adaptive significance, is possibly a relict from an earlier polyphenism where alternative solutions were triggered by alternative conditions to which the animal could be exposed in a region of interface. This agrees with the ecological scenario proposed by Jablonski (2005) for the evolution of many groups of marine invertebrates. Systematically looking through the fossil record, most anatomical innovations apparently arise onshore, i.e. in a more variable environment, while the more stable offshore environments are mostly colonized by largely stabilized forms.

The unstable and unpredictable conditions of seasonally desiccated swamps, where survival may strongly depend on the simultaneous or sequential availability of organs for both gas exchange in water (gills or equivalent) and in air (lungs or tracheae), provide a likely scenario for the early evolution of terrestrial tetrapods, as well as for the origin of pterygote insects, and perhaps even endopterygotes (Omodeo *et al.* 1980). But even if the latter suggestion is not tenable, in the light of current understanding of insect phylogeny (e.g. Wiegmann *et al.* 2009), the habitats hosting modern representatives of basal holometabolous lineages suggest temperate conditions subject to strong seasonal variation. Within the Hymenoptera, this is true of members of the basal phytophagous clades in the Symphyta. Seasonal, stressful conditions are also those of arid, desert regions, where the transition to hypermetabolism of blister beetles has likely evolved.

7. FUTURE RESEARCH TARGETS

Comparing transcription profiles from different developmental stages throughout a complex life cycle with those from alternative phenotypes in closely related polyphenic animals is likely to offer critical evidence on which to evaluate our hypothesis. Data from suitably chosen taxa are not yet available, but relevant information is emerging from studies of life cycle transcriptomes of holometabolous insects (*Drosophila melanogaster*, Arbeitman *et al.* 2002; *Anopheles gambiae*, Koutsos *et al.* 2007), as well as from comparisons of transcriptome dynamics between alternative phenotypes in polyphenic nematodes (normal versus dauer larva in *C. elegans*; Holt 2006) or between alternative larval types normally expressed by poecilogonous animals (planktotrophic versus lecithotrophic larvae of the polychaete *Streblospio benedicti*; Marsh & Fielman 2005).

Interestingly, results of two studies (dealing admittedly, with very different organisms rather than with

two directly comparable taxa) converge in singling out the earliest post-embryonic stages as a segment of developmental history which is particularly prone to polyphenism or to diverge from later stages through changes in transcription profiles that probably correspond to (i) changes in the activity of genes for transcription factors (early versus late larvae in *Anopheles*; Koutsos *et al.* 2007) and (ii) increasingly strict control of transcription in what is likely the more derived phenotype (lecithotrophic larvae of poecilogonous polychaetes; Marsh & Fielman 2005).

These differences could be compatible with an origin of interstage differences via environmental modulation of development, whereas the very distinctive patterns of transcription found in mosquito pupae are clearly of different nature. Here, many expressed genes are implicated in the extensive histolytic processes required to combine the bodily architecture of the larvae, which has been selected for increasing divergence from the adult, with the arguably more conserved bodily architecture of the latter (Heming 2003; Minelli *et al.* 2006).

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