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Cooking up the perfect insect: Aristotle's transformational idea about the complete metamorphosis of insects

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Aristotle made important contributions to the study of developmental biology, including the complete metamorphosis of insects. One concept in particular, that of the perfect or complete state, underlies Aristotle's ideas about metamorphosis, the necessity of fertilization for embryonic development, and whether morphogenesis involves an autonomous process of self-assembly. Importantly, the philosopher erroneously views metamorphosis as a necessary developmental response to lack of previous fertilization of the female parent, a view that is intimately connected with his readiness to accept the idea of the spontaneous generation of life. Aristotle's work underpins that of the major seventeenth century students of metamorphosis, Harvey, Redi, Malpighi and Swammerdam, all of whom make frequent reference to Aristotle in their writings. Although both Aristotle and Harvey are often credited with inspiring the later prolonged debate between proponents of epigenesis and preformation, neither actually held firm views on the subject. Aristotle's idea of the perfect stage also underlies his proposal that the eggs of holometabolous insects hatch 'before their time', an idea that is the direct precursor of the much later proposals by Lubbock and Berlese that the larval stages of holometabolous insects are due to the 'premature hatching' from the egg of an imperfect embryonic stage.

This article is part of the theme issue 'The evolution of complete metamorphosis'.

1. Introduction: Aristotle, developmental biology and metamorphosis

The Greek philosopher Aristotle (Aristotelis, Ἀριστοτέλης, 384–322 BCE), has long been considered to have been the first 'real' biological scientist [1–3] and was also the first person known to have seriously enquired into the nature and causes of animal metamorphosis.

Aristotle was interested in the complete metamorphosis of insects not only because he was continually curious about the variety of animal life and form, but because he recognized that the radical transformation of an externally simple worm-like insect larva to a highly complex adult insect offered an opportunity to test out his ideas about animal reproduction and embryonic development. As will be shown below, the philosopher believed that metamorphosis and the mystery of the spontaneous generation of life were linked. For Aristotle, explaining metamorphosis was an opportunity to explain the origin of life from non-living material.

In one sense, his most important contribution was simply to assert that metamorphosis

> which may well cause surprise to many people, is really quite regular and normal[1]. [4] [GA 758b28]

In other words, he did not ascribe metamorphosis to magic or hidden divine causes. But the philosopher also introduced an important idea into thinking about morphogenesis and metamorphosis that had profound effects on the

way that much later scientists approached these subjects. This is the concept of the *perfect* condition and is the subject of this paper. In both ancient and modern Greek, the word is Teleos (*τέλειος*), which means 'perfect', 'complete' or 'finished'. The word is important in this paper because in Aristotle's view, complete metamorphosis is a developmental process that allows an imperfect animal to attain the condition of perfection. Aristotle's idea of perfection was an important influence on the views of the anatomists of the seventeenth century Scientific Revolution, who are generally credited with revealing the significance of complete metamorphosis in the lives of insects; Aristotle's ideas continued to influence biological scientists until the nineteenth century, but because the philosopher was explicit in supposing that development is a 'teleological' process (i.e. one that is driven towards a predetermined purpose or end, the production of the 'perfect' organism), they have not in recent times inspired much scientific enthusiasm.

But it is also possible to regard 'perfect' as being simply a descriptive adjective, meaning that morphogenesis is now complete and no further morphological change will occur, and I argue that in this sense, Aristotle's idea that morphogenesis can only progress towards completion when certain internal conditions are satisfied remains a useful one. Without wishing to imply that Aristotle was in any way able to anticipate our present understanding of animal reproduction and development in terms of molecular genetics and biochemistry, I nevertheless suggest that his ideas are indeed precursors of our current biological understanding of development and metamorphosis, in exactly the same way as those of Democritus anticipated modern ideas of the nature of matter by positing the existence of atoms [7].

Aristotle's ideas about development and metamorphosis were regarded at the time by the seventeenth century scientists from whom our present paradigm of these subjects derives, as the direct precursors of their own investigations [8]. Harvey [9], Malpighi [10] and Swammerdam [11] cited Aristotle on almost every page of their works. In modern times, the philosopher's scientific work has frequently been dismissed as seriously flawed and only semi-scientific [12,13]. It must be admitted that Aristotle's science had limitations. As a philosopher, Aristotle was primarily interested in the *purpose* and *causation of* natural phenomena, by which is meant *why* and *how* they come about. To examine these questions, he employed direct observation, and also interrogated others who he believed were reliable informants, thus assembling an extensive database of natural phenomena in which he attempted to discern patterns. As Leroi has noted [2], this procedure was used to investigate causation through correlation and extrapolation in essentially the same way as what we now call the comparative method. What Aristotle did not do, however, was to test his ideas about causation using experiments in which he interfered with the proposed causes; inevitably, this caused him to draw erroneous conclusions [2,12,13]. Aristotle's interest in purpose was arguably even less scientific than his interest in causes, and he relied mostly on teleological arguments, reiterating again and again that the final cause of something is 'that for the sake of which a thing is done' [14]. It might well be observed here that this approach is not so different to the *modus operandi* of those evolutionary biologists who attribute 'adaptive' function to heritable traits, on the similarly circular argument that these traits must be adaptive or they would not persist. Without an experimental test, the value of such ideas is at best questionable [15].

Do these limitations of some aspects of Aristotle's ideas about animal development mean that we should ignore his contributions to understanding the biology and evolution of metamorphosis? I contend that it is always a good thing to know where today's ideas originally came from, even if the original versions have been superseded.

2. Aristotle and the energetics of animal development

Aristotle was interested in complete metamorphosis because he was investigating animal development. He believed that an insect pupa was like an egg, except that the animal developing within it was much larger and therefore easier to study. Doubtless like countless others before and since, Aristotle wondered how a complete animal can be assembled from an apparently almost formless egg. The process is astonishing, because outside of the realm of living things, highly complex structures, whatever they are made of, do not normally self-assemble from simpler materials. Yet when a new animal is generated, order is apparently being created out of disorder. Understanding the problem of what Aristotle called Genesis (*γένεσις*, 'generation'), a discipline encompassing both reproduction and embryonic development, thus promised to supply an answer to the nature of life.

We now recognize that the problem of generation is fundamentally one of entropy [16]. By creating a highly structured assembly of complex components out of simpler disordered materials, living systems locally reduce entropy at the expense of increasing the total entropy of the system and its surroundings. During growth and development, the organism must 'pay' for the generation of additional living material by dissipating energy, the interconversion of energy and entropy being mediated by metabolic chemical reactions; another way to put this is to say that generation is energetically costly [17]. Ideas like this were of course entirely unknown to Aristotle. Nevertheless, in his investigations of development, he followed what we can now recognize as a thermodynamic approach to the problem: hypothesizing that the transformation of an imperfect offspring to a perfect one requires what we would now call 'energy'. Aristotle did not have a concept of energy in the modern sense of the capability to perform work; instead he referred to Dynamis (*Δύναμις*—literally 'capability' or 'power'), an attribute that had the potential to cause diverse kinds of change; these effects of Dynamis were sometimes characterized as 'exchange' (*μεταβολή*) or 'activity' (*ενέργεια*), and manifested themselves as 'heat' [Thermon (*θερμόν*)], or sometimes as 'movement' [Kinesis (*κίνησις*)]. For Aristotle, a clue to this involvement of energy in development was doubtless supplied by the well-known fact that to hatch a hen's egg, you have to keep it warm.

Aristotle was interested in fertilization; he explained how an energetic agent present in the seminal fluid supplied by the male might cause the change in form of the materials supplied by the female (he calls these materials the 'fetation') by likening its action to that of a carpenter on the wood that is being worked. He says that rather than the additional new material, this is a question of action (i.e. a supply of energy

—here Aristotle calls it 'movement') and information (he calls it 'soul', best regarded as 'form and knowledge'):

> this semen is not a part of the fetation as it develops. In the same way nothing passes from the carpenter into the pieces of timber, which are his material, and there is no part of the art of carpentry present in the object which is being fashioned; it is the shape and the form which pass from the carpenter, and they come into being by the movement in the material. It is his soul, wherein is the form, and his knowledge, which cause his hands … to move in a particular way…; his hands move his tools and his tools move the material. [4] [GA730b11-19]

Famously, in many passages of his book *Generation of animals* [4], the philosopher also likens embryogenesis to cooking. Supplying 'heat' to the materials of which an egg is formed, he argues, causes them to reorganize first into the form of the embryo, and then as the cooking continues, into the adult animal. Using a simple analogy, he points out that a familiar material like milk can be 'set' or curdled when it is heated [4] [GA 729a11-14]. He argues that since nothing is added to the milk when it is heated, the altered form of the milk when it has been set must from the start have been inherent in its own nature or essence, the change in form that occurs when it is heated merely being encouraged or permitted by the cooking process. This is entirely compatible with our own modern ideas about how protein structure is determined by its amino acid sequence; all that the heat treatment does is to allow the milk proteins to reorganize themselves into a lower energy state than when they were initially synthesized. Remarkably, Aristotle goes on to point out that setting of milk does not have to be achieved by cooking but can be produced by adding a rennet or setting agent (he particularly mentions fig juice, long known to have the property of curdling milk). He says that it is in the nature or essence of the fig juice to set the milk, just as it is in the nature or essence of the milk to be coagulated. It is *as though* the rennet supplies heat to the milk. We now know that the setting agent in fig juice is an enzyme, the cysteine endopeptidase ficain, which cleaves the milk protein casein, altering its molecular shape, and rendering it insoluble [18]. The point of this story is that Aristotle is here envisaging that the tendency to 'set' (i.e. to develop) is inherent in the materials of the egg, and is released or catalysed by fertilization. Interestingly, Aristotle noted that the fertilizing agent in the semen would not be consumed or incorporated into the offspring:

> The physical part of the semen, being fluid and watery, dissolves and evaporates; and on that account we should not always be trying to detect it… as an ingredient of the fetation when that has set and taken shape, any more than we should expect to trace the fig-juice which sets and curdles milk. [4] [GA 737a12-17]

Of course, embryogenesis involves much more than such changes to the structures of one or more egg proteins, and Aristotle was aware of this. He recognized that many additional structural and spatial changes would be sequentially required to shape the form of the developing animal. In still another analogy, he compared the ensuing sequence of developmental events that occurs during embryonic morphogenesis to the sequences of movements performed by classical Greek temple automatons. The precise nature of these religious machines is not now known [19], but it is clear from Aristotle's discussion that they had parts connected to each other by levers and pivots, were powered by stored energy, and were set in motion by an operator from outside. This being so:

> the parts of these automatons, even while at rest, have in them somehow or other a potentiality, and when some external agency sets the first part in movement, then immediately the adjacent part comes to be in actuality. [4] [GA 734b10-13]

In a similar fashion, argues Aristotle, once embryogenesis has been initiated by fertilization, one thing follows another without further intervention by the initiating agent. Since we now know that much of the mechanics of embryogenesis relates to changes in the recruitment of high-level transcription factors, we may suppose that a stereotyped and progressive programme of transcriptional changes is an important part of the process. There is every reason to suppose that this programme of change is indeed inherent in the developing organism and could be set in motion in an automaton-like way by a primary activating agent associated with fertilization, and then coordinated by subsidiary activating agents already present within the undeveloped embryo.

3. Aristotle and fertilization

Aristotle has now established a plausible model for the mechanism that sets embryonic development in motion. But in the case of animal generation, where does the 'heat' or 'movement' required to provoke the 'setting' of the raw material of the embryo come from? He insists that this is supplied exclusively by the male parent, noting that eggs produced and laid by female animals do not develop further unless they are fertilized by a male. Therefore, he argues, the heat (or other form of energy) that does the cooking must be supplied by the male, contained within the seminal fluid.

Aristotle now supposes that just as fig juice comes from a fruit that has matured in the heat of summer, semen is a substance that has matured in the heat of a male animal's testes. He does not know what it is about the male that allows this to happen, but he again draws the parallel with cooking and supposes that the male is 'hotter' than the female, allowing the maturation of semen to take place. What he is really saying is that it is in the nature or essence of the semen to contain something (which he likens to 'heat') that has the power to initiate the 'setting' of the egg-material, and which is not contained in the egg itself.

What is this 'heat' in the semen? Aristotle attempts to explain it in a number of ways. Most importantly, he says that it is supplied by an attribute of the semen called Pneuma (*Πνεύμα*) or 'breath'. This Pneuma is an agent or vehicle, a kind of vector for the factors that actually put into effect the morphogenetic processes shaping the animal. Its effects are mediated by the heat and movement that it mobilizes. These are not literally heat and movement, just as Pneuma is not literally the 'breath' of the animal concerned, nor is it breathed in from outside; its downstream effects are evidently energetic in some sense.[2] While Aristotle's terminology is awkward in the context of modern science, it should be noted that these concepts can relatively easily be accommodated in terms of a model in which energy-yielding cellular processes are used to effect developmental change during embryogenesis.

The scheme just described not only attempts to explain in mechanistic terms the mystery of how the complex structures of living things are formed, but also supplies an answer to the problems of sex and its place in the life of animals. Unfortunately, however, a serious problem emerges very quickly. This is because not only was it known to the philosopher

that some animals generate offspring without being seen to copulate, but it was also generally believed at that time that some forms of life were generated spontaneously from non-living materials.

How could Aristotle's 'cooking' model of embryonic development be reconciled with these two problems? The answer is that the philosopher sidestepped the problem by supposing that lack of fertilization and spontaneous generation are actually the same thing, and that complete metamorphosis is the natural consequence of them both. Aristotle's interest in metamorphosis can thus be seen to stem very largely from his need to accommodate the phenomenon of spontaneous generation in his scheme of animal development. To explain how he attempted to solve the problem of spontaneous generation, we must introduce the idea of the perfect condition.

4. Aristotle: complete metamorphosis and the perfect condition

Aristotle's idea of the perfect state of an animal is a philosophically hybrid concept incorporating Plato's notion of the definitive or essential but abstract version of the form (i.e. morphology) of an animal, as well as the typically Aristotelian element of the causal factors involved in the generation of that form. Unfortunately, Aristotle does not anywhere in his surviving writings produce a single statement that defines exactly what he means by 'perfect' in the context of animal generation. A general reading of *Generation of animals* [4] and *History of animals* [5,6] in both of which this word is used many times, however, reveals that Aristotle regards the perfect condition as that state of an animal which enables us to discern by its bodily form the species to which it belongs (i.e. to recognize it for what it is). Perfection is also an enabling condition, which allows the animal in question to generate another member of the same kind in the same perfect form:

> Some animals bring their young to perfection and bring forth externally a creature similar to themselves…. [4] [GA 732a26-27]

A phrase that Aristotle uses often to explain this, is that perfect offspring have 'the same name and nature' as their parents. Perfect also means 'adult in form'. Interestingly, in the context of complete metamorphosis, entomologists sometimes still use the term 'perfect' to mean 'adult' [20].

As noted above, the Greek word Teleos also means 'complete', in the sense of 'finished', and this means that an animal in this condition has no need to change in form or grow any further once it is 'perfect'. Aristotle says:

> …some lay their eggs in a perfected state … eggs which once they are laid do not grow any more. [4] [GA 732b1-6]

> Some creatures' eggs are imperfect when laid … which become perfected i.e. grow, outside the creature which produces them. [4] [GA 718b6-8]

This second idea of perfect and imperfect eggs corresponds well to the well-established modern contrast between the cleidoic (shelled) eggs of birds and reptiles, which do not grow, and the non-cleidoic (shell-less) eggs of other vertebrates, which increase in size by taking up water [21]. But the presence or absence of a size change is an unsatisfactory component of Aristotle's thinking about the perfect state, because although the philosopher thinks that eggs that grow in size after being laid but before hatching must be lacking in perfection, he overlooks the criterion of growth when it comes to growth in size of the animal once it has hatched. Although Aristotle is aware that it would be very unusual indeed for an animal to be born or to hatch at its full adult size, he nevertheless considers the immature but adultiform animals that hatch from perfect eggs to be perfect themselves in form even if they are not yet 'perfect in size'. He says:

> No animal brings forth young that are perfect in size, because they all grow in size after they are produced. [4] [GA 733b3-4]

Another aspect of Aristotle's conception of the perfect condition, of which the significance has already been noted above, is that (quite incorrectly) Aristotle asserts that perfection is something to do with body temperature, as follows:

> The more perfect animals are those which are by their nature hotter. [4] [GA 732b32-33]

Another complication is that the philosopher also thinks that a hierarchy of perfection exists, in which the most perfect animals are at the top, with others below them according to their degrees of perfection. In allocating status in this hierarchy, Aristotle ranks animals into categories (I list them along with their modern names) as follows: (i) humans; (ii) viviparous animals (e.g. mammals) that are not (he thinks) derived from eggs; (iii) viviparous animals (e.g. some fish) that are derived from retained eggs; (iv) oviparous animals (e.g. birds, reptiles, hemimetabolous insects) that produce perfect eggs (i.e. they do not grow before hatching externally); (v) oviparous animals (e.g. teleost fishes, Crustacea, Cephalopoda) which copulate and thereby produce imperfect eggs that nevertheless 'reach perfection outside the parent by means of growth'; (vi) insects (he means here holometabolous insects) and other animals which generate larvae, either with or without the production of eggs, by means that he believes do not involve copulation. [4] [GA 733a34–733b17]

Aristotle explains this hierarchy by appealing to the same causative factors that we have already seen to preside over the acquisition of the perfect state. In particular he supposes that progress from the lowest form of vegetative existence to progressively higher levels of organization and behaviour is due to the possession of a hierarchical sequence of different parts or faculties of something that he calls Psyche (*Ψυχή*) or 'soul', which (as used here) means the actual (i.e. realized) essence of the animal.

It is this hierarchical way of thinking about insect life cycles in terms of 'perfection' that leads Aristotle to the (to us) counterintuitive conclusion that because hemimetabolous insects are born perfect, whereas their holometabolous relatives are born imperfect and must therefore acquire their perfection in later life, the latter must be the basal (i.e. undifferentiated) form from which the former are derived. He says:

> In a way, it looks as though practically all animals produce a larva to begin with, for the fetation in its most imperfect state is something of this sort; and in all the Vivipara and all the Ovipara that produce a perfect egg, the fetation in its earliest stage is still undifferentiated and is growing and is just the sort of thing that a larva is [4] [GA 758a33-37]

This idea, reminiscent of Haeckel's Biogenetic Law of recapitulation [22], certainly does not reflect the true course of evolution, since it is now quite clear that the Endopterygota are in fact derived from the basal exopterygote condition [23], thus the opposite of what Aristotle had thought.

5. Aristotle: inheritance and metamorphosis

Aristotle's account of embryonic development focuses our attention on the limited understanding of the inheritance of form and its relationship to the taxonomy of living things that was possible at that time. Aristotle developed his own theory of inheritance, in which the species of organism into which the embryo develops depends on the inheritance of its Eidos (Εἶδος) or form (i.e. its essential species-level characteristics) from the male parent. Eidos arises during development through the action on passive materials derived from the female parent of an organizing active principle (Pneuma and all that it implies—see above) that is present in the seminal fluid. This sexually divergent aspect of Aristotle's theory of inheritance is usually termed 'Reproductive Hylomorphy' [24].[3] Aristotle says:

> The male provides the 'form' and 'the principle of movement', the female provides the body, in other words the material. [4] [GA 729a9-12]

But what of those organisms that Aristotle believes to be derived from unfertilized eggs, and those organisms that he supposes are generated spontaneously from inanimate material? Clearly, because in each of these cases they would lack those aspects of form that are supposed to be determined by a male parent, Aristotle's principle of reproductive hylomorphy dictates that such offspring cannot belong to the same kind as either their male or their female parent. The philosopher duly decides that those kinds of organisms that are generated 'without copulation' (i.e. by what he believes to be an asexual process of generation) must therefore at least initially have a different form or essence to the parents. They must instead, says Aristotle, undergo a process of metamorphosis that allows them to transform from the incomplete (imperfect) form of the larva to the complete (perfect) from of the adult. During the process, essential form (conferred by Pneuma) that was previously absent is acquired by the metamorphosing animal in some way that is different from fertilization. He says:

> Further, some animals are formed neither from creatures of the same kind as themselves nor from creatures of a different kind, examples are flies and the various kinds of fleas as they are called. Animals are formed from these it is true, but in these cases, they are not similar in character to their parents; instead we get a class of larvae. [4] [GA 723b3-7]

The importance of this difference in view of the plasticity of an organism's essential nature can hardly be exaggerated. It is a fundamental cause of the divide between Aristotle's biology and our own. The morphological species concept that has been current in biological science from the time of Linnaeus onward completely depends upon the idea that every living organism is a member of only one species and is generated only from the same species of organism [25]. It is controversial whether or not the species concepts of Aristotle and Linnaeus, and also of modern biology, are philosophically essentialist ideas [26–31], but it is incontrovertible that the Linnean species is dependent on like breeding like. We now take it for granted that the nature of an animal is defined by its parentage. But, for Aristotle, it is evident in the context of complete metamorphosis that the Eidos of an animal is not necessarily defined by a single essence at all, and that in metamorphosing animals, the need to metamorphose is due to the failure of the parent to transmit the essential nature that defines the adult form. Some organisms, he says, notably insects that undergo complete metamorphosis, adopt more than one form during their lives, and therefore must possess more than one type of Eidos. Moreover, says Aristotle, such animals obviously do not breed true, because the larval forms generated by such insects are quite unlike their parents. And before these larvae can become like their parents, they must transform into a different form of animal, only then acquiring the competence to generate further offspring (figure 1*a*).

6. Aristotle: insects that produce perfect offspring

By contrast with holometabolous insects, the progeny of hemimetabolous insects, like those of the sanguineous or 'blooded' animals (in Aristotle's scheme, those that have red blood, such as both mammals and birds) are already 'perfect' in that they are either born or hatch to produce an immature animal that can grow into an adult without further major morphological transformation, except growth in size. To be more accurate, in the case of the Hemimetabola this means 'almost without', since the immature insect's wings and reproductive organs differ significantly in shape and size from the those of the adult. Aristotle says:

> As regards insects, some of them copulate, and in those cases the young are generated from animals which are the same name and nature as themselves, just as happens in the blooded creatures; instances of this are locusts, cicadas, spiders, wasps, ants. [4] [GA 721a3-5]

Aristotle refers here to members of orders that we would today class as hemimetabolous insects (namely locusts and cicadas) as well as other invertebrates (spiders). Never mind that he is wrong in considering wasps and ants to be of this kind; we can see what he is driving at: the immature forms of locusts, cicadas, and spiders are indeed of the same kind as the adult forms.[4]

Notice that Aristotle links his statement that insects of this kind produce offspring with 'the same nature and name as themselves' (i.e. that the immature insects are already perfect) with the assertion that they 'copulate' (it is implied that other kinds of insects do not). The significance of the last point will become clear below. Perhaps confusingly, the metamorphosis of hemimetabolous insects like these is nowadays often designated as 'incomplete', but to Aristotle it was no metamorphosis at all because the nymph has the 'same nature and name' as the adult, in other words they are already 'complete'.

Aristotle is not always very clear on whether he thinks that this kind of insect is generated as a perfect offspring by means of an egg. He clearly says that grasshoppers do copulate and lay eggs [5] [HA 555b18-19]. But he then mistakes what is in fact the developing egg of a locust for a worm-like larva (this is surprising because if what he says were true it would mean that he would have to classify a locust as belonging to the class of insects that he says are generated spontaneously). He says:

> [Locusts] deposit their ova in one spot, so as to make it appear like a honeycomb. As soon as they have deposited their ova, egg-like maggots are formed, which are covered with a thin coating of earth like a membrane, and in this they are matured. The young are so soft as to collapse if they are only touched. They are not produced on the surface, but a little below the surface of the soil; and as soon as they are matured, they escape from the coat of

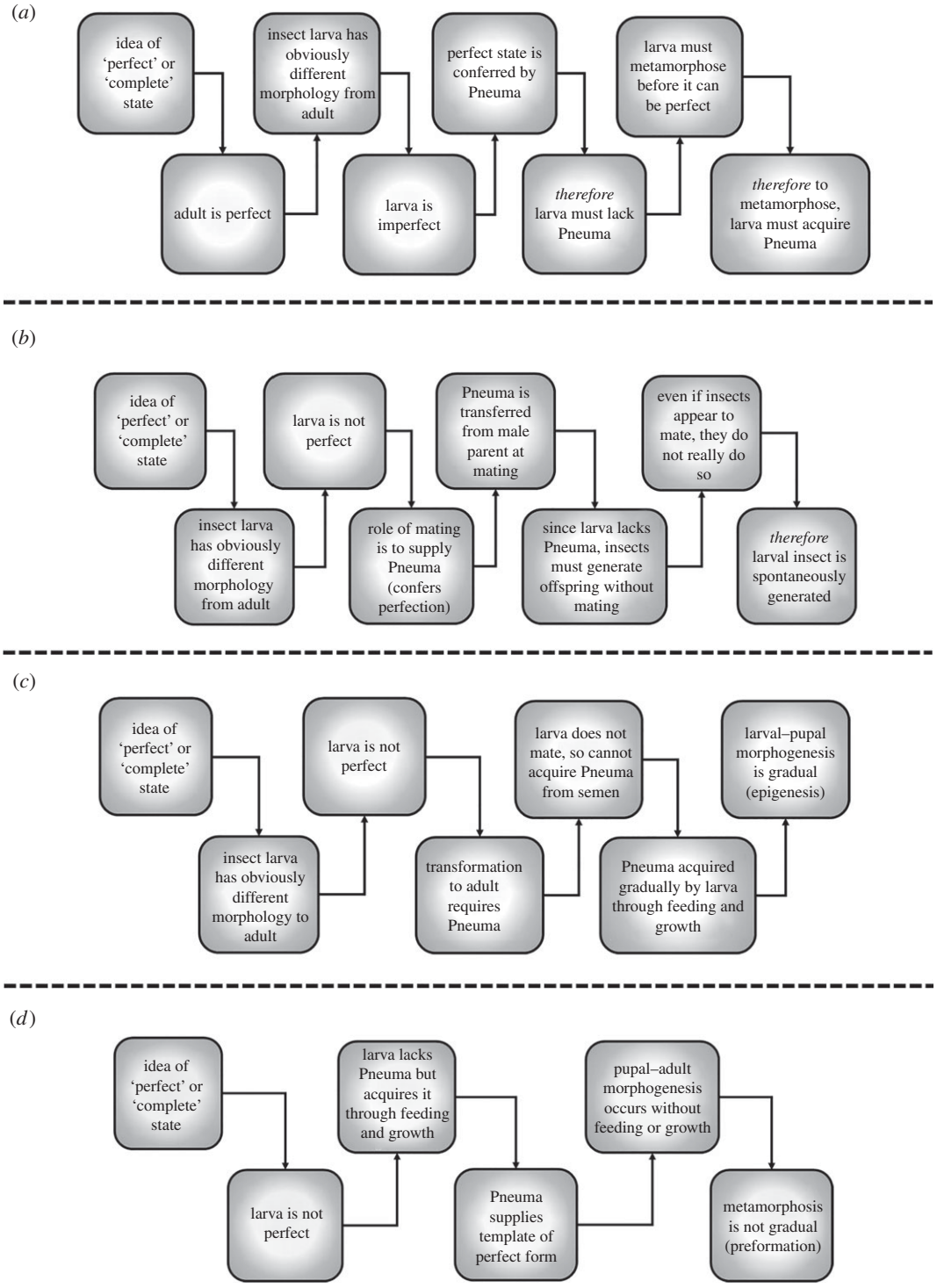

Figure 1. Aristotle's concept of the perfect or complete state and its implications. (*a*) The concept of the perfect state leads Aristotle to conclude that a holometabolous insect larva differs from the adult of the same species because it lacks Pneuma. (*b*) Aristotle concludes that because holometabolous larvae lack Pneuma they must be generated spontaneously (i.e. without fertilization). Even if these insects appear to mate, they do not really do so. (*c*) Aristotle recognizes that larval–pupal morphogenesis is a gradual process that involves feeding and growth, and in which perfect form develops as a result of the gradual accumulation by the larva of Pneuma from outside of itself. (*d*) Aristotle considers that pupal–adult morphogenesis is an abrupt process that does not involve feeding and growth, and in which perfect form is generated from a template provided by Pneuma. Aristotle contrasts this with the gradual development of the perfect state in (*c*). Note, however, that although Harvey later regards non-gradual pupal–adult transformation as necessarily non-epigenetic, contrasting it with gradual larval–pupal development, Aristotle does not draw such a distinction.

> soil in which they are enclosed as small black locusts. Their skin is subsequently ruptured, and they then attain their full size. [5] [HA 555b22-30]

This description is startlingly accurate, giving the strong impression that the philosopher has observed it at first hand. Locusts do indeed lay their eggs underground within a foamy proteinaceous capsule. The 'egg-like maggots' described by Aristotle are actually pharate first instar larvae, developing within an embryonic cuticle inside the egg. They subsequently migrate to the surface and undertake their first free-living ecdysis to hatch as first instar larvae that look like little locusts [32].

7. Aristotle: insects that produce imperfect offspring

In considering other insects (they are the majority) that do not conform to the above pattern, Aristotle again appeals to the idea of a hierarchy of perfection, asserting that:

> since an actual animal is something perfect whereas larvae and eggs are something imperfect, Nature's rule is that the perfect offspring shall be produced by the more perfect sort of parent. [4] [GA 733a3-6]

He applies this idea to the larvae of holometabolous insects, which in his view are not 'perfect' or 'complete' because they do not look like adults. Whether or not these creatures are produced from an egg (more on this below) their free-living immature form is that of a 'worm' or larva (Scolex (*Σκολήξ*)) that has a completely different appearance from the adult. Instead, these imperfect larval insects, being *of a different kind* to the adult, feed and grow and eventually undergo a metamorphosis in order to become a pupa (a stage that is perfect, because it can give rise to an adult without further transformation). On multiple occasions the philosopher directly compares larvae and pupae to eggs, stating that these eggs initially lack perfection but acquire it as they feed and grow:

> The larva, while it is yet in growth, is a soft egg. [4] [GA 758b21-22]

> All these larva-like objects, when they have advanced and reached their full size, become as it were an egg: the shell around them gets hard, and they remain motionless during this period. This is clearly to be seen with the larvae of bees, wasps and caterpillars. [4] [GA 758b15-19]

> All of these [he is referring to apparently spontaneously generated insects such as clothes moths] first have the nature of a larva, then they remain motionless once the covering has solidified around them; after that the covering bursts and there emerges, as from an egg, an animal which, at this its third genesis, is at last perfected. [4] [GA 758b24-27]

8. Aristotle: animal generation with and without eggs

It was noted above that Aristotle is careful to note that some animals copulate, while some do not. The reason for his interest in this issue concerns the question of whether all animals hatch from an egg. Some 2000 years later William Harvey asserted that generation does indeed always proceed from an egg (see below), but Aristotle came to a very different conclusion.

In the case of 'animals that copulate' Aristotle recognizes that some sanguineous animals (notably all mammals, but also some cartilaginous fish) are viviparous, and because he cannot see that eggs are involved in the process, he erroneously concludes that these animals must be generated entirely without the involvement of eggs. Even when he dissects the body of a pregnant mammal or dogfish, he cannot find an egg because it is too small to be seen without magnification. He contrasts this situation with that of 'lower' blooded animals (birds and reptiles) which produce large easily visible shelled eggs. He calls such eggs perfect because they do not increase in size before hatching.

Additionally, Aristotle knows that there are other vertebrates (i.e. Amphibia and most fish) that lay eggs which clearly develop and grow in size before hatching; these eggs are therefore not perfect offspring. It is significant in the philosopher's view that such animals do not fertilize their eggs internally, but externally. He explains the adaptive value of this state of imperfection by pointing out that for ecological reasons (the high rate of mortality due to predation) these creatures need to produce very large numbers of eggs that cannot easily be accommodated within the female's body, and so they are expelled at an early stage of their formation. However, the fact that they are subsequently fertilized allows them to become perfect as a consequence and to generate offspring that look like the parents. It seems to me very likely that it was this line of thought that led to Aristotle's idea that fertilization is necessary to the acquisition of the perfect state.

But Aristotle also knows that some invertebrates (e.g. hemimetabolous insects) lay eggs that do not grow in size before hatching. Since all these animals enter free-living life looking like miniature adults, he considers their eggs to be perfect, like those of birds and reptiles. Aristotle's language on this point is sometimes less than helpful, because in classifying the various generative methods he does not always distinguish between an imperfect egg and a larva (in his view they are really the same thing). But in the following passage, he makes the difference clear; it is based on whether the offspring is supplied with nourishment internally (this is an egg) or externally (not an egg):

> Some animals bring their young to perfection and bring forth externally a creature similar to themselves—e.g. those which are externally viviparous; others produce externally something which is unarticulated and has not yet assumed its proper shape. In the latter class those which are blooded lay eggs, those which are bloodless produce either eggs or larvae. The difference between an egg or a larva is this: an egg is something from *part* of which the new creature is formed, while the remainder is nourishment for it; whereas in the case of the larva, the *whole* of it is used to form the whole of the offspring. [4] [GA 732a26-33]

Thus insects (otherwise considered by Aristotle to be a single kind of animal) pose the philosopher a problem, because although some insects produce objects that look like eggs and satisfy his criterion of internal nourishment, and must be perfect because they hatch as perfect offspring, other insects generate only imperfect eggs or even (where the philosopher has no evidence of eggs at all) larvae that are apparently directly generated with no intermediate egg stage.

What differentiates these two subclasses of insects? Aristotle solves the difficulty by supposing that the apparently perfect eggs of some insects are not really 'eggs' at all (they are larvae or 'fetations' that metamorphose directly into perfect miniature adults). He says:

> Of bloodless animals, insects produce a larva; this holds good both for those which are formed as a result of copulation and those which themselves copulate. [4] [GA 732b10-12]

> Insects all produce larvae. Now all insects are bloodless, and that actually is why they are externally larva-producing. [4] [GA 733a25-27]

> The fifth class of creatures, which are the coldest of all, do not even lay an egg directly themselves, but the formation of their egg takes place outside the parent. [4] [GA 733b11-13]

All this is crucially tied up with Aristotle's idea of a hierarchy of perfection. Members of the class of animals that lay eggs (whether they are insects or not) are not so imperfect as those (such as insects) that produce worm-like progeny, which occupy the lowest position in the hierarchy of

perfection, lower even than the eggs of those creatures 'that copulate'. Even if the progeny of non-copulating insects and similar animals appear to emerge from structures that look like eggs, Aristotle says that they are not really eggs.

Because of his ideas about how perfection is conferred (i.e. as the result of fertilization), Aristotle concludes that animals like this (i.e. holometabolous insects), which do not generate perfect offspring, must be generated spontaneously, i.e. without copulation. The philosopher does not consider the criterion for inclusion in this class to be absence of evidence for copulation of the parents or even of the presence of eggs; as we will see below, he dismisses such evidence as inadmissible even when he sees it with his own eyes. Instead, he simply asserts that generation must be spontaneous whenever the end of larval life is succeeded by metamorphosis, which is the process that allows an incomplete or imperfect animal to achieve the perfect or complete form. This is the logic that explains why we still designate this type of transformation as 'complete metamorphosis'.

Aristotle now goes even further; he states that because it is the equivalent of the egg stage from which a perfect animal hatches, the pupal stage of a metamorphosing insect is in fact the functional equivalent to an egg. He says of insects of this kind:

> …we are bound to reckon caterpillars … as a form of larva. True, some of these, and many belonging to other insects, would appear to resemble eggs on account of their circular shape; but our decision must not be determined by their shape nor yet their softness or hardness… but by the fact that the whole of the object undergoes change—the animal is formed out of the whole of it and not some part of it. [4] [GA 758b9-15]

> What happens is that Insects first produce a larva, then the larva develops till it becomes egg-like (what is called the chrysalis is really equivalent to an egg[5]); then out of this an animal is formed, and it is not until this third stage in its series of changes that it reaches the end and perfection of its generation. [4] [GA 733b11-17]

9. Aristotle: spontaneous generation and metamorphosis

As we have seen from the above, Aristotle thus not merely fails to dismiss the idea of spontaneous generation of living from non-living matter, specifically commenting without any apparent reservation that flies are generated *de novo* from the carcasses of dead animals, but he actually incorporates the idea of spontaneous generation into his scheme for the reproduction of the single most numerous and diverse category of animals.

Did Aristotle really believe in spontaneous generation? Most Aristotelian scholars have concluded that this was in fact the case, usually excusing the philosopher's apparent credulity on the grounds that this was an understandable error given the almost universal belief in the spontaneous formation of some forms of life in ancient times [33]. If this is all that is behind it, however, then it is hard to avoid the conclusion that the philosopher was culpable in failing to test the idea of spontaneous generation experimentally; it would have been easy, even without sophisticated apparatus, for Aristotle to interrogate his hypothesis simply by protecting a putrefying animal carcass from ovipositing flies with a covering cloth, just as Francesco Redi was to do almost 2000 years later [34] (the story of Redi's experiments is nicely told by Cobb [8]). An objection to such a conclusion is of course that we cannot retrospectively expect Aristotle to do experiments, because the experimental approach to investigation had not then been invented. Leroi [2, pp. 362–363 and notes thereon] is convincingly sceptical about the extent to which Aristotle employed or even understood the idea of an experiment.

A notably different view, however, is that of Zwier [35], who sets out to construct what she calls a 'more charitable view' of Aristotle's erroneous views about spontaneous generation. She points out that the philosopher goes to considerable lengths [4] [GA 762a37–763a25] to interrogate critically the idea of spontaneous generation, using the same methods of questioning and logic that he employed in considering other problematic issues. It appears that despite his best efforts, the philosopher simply came to an answer that we now know to be wrong.

Let us also be charitable. The ancient Greek philosopher's text is not always clear, and he may simply have been saying that fertilization is not always a prerequisite for the generation of a new animal. This is indeed absolutely true, and parthenogenesis is now known to occur widely in the animal kingdom [36], including in many insect species from most orders [37,38], although we have to note that Aristotle is highly unlikely to have encountered any example and known it for what it was. Even in the case of honeybees, on which he writes at length (see below), Aristotle fails to distinguish the sexual generation of workers from the parthenogenetic production of drones [4] [GA 759a8–761a37].

But even if Aristotle is not really convinced by the idea of spontaneous generation from material that did not originate in flies, and he is indeed saying that flies arise from eggs derived from female flies but without fertilization, then we have to ask where do those eggs come from?

10. Aristotle: fertilization and metamorphosis

The above discussion is relevant to Aristotle's treatment of insect metamorphosis, because of the philosopher's erroneous assertion that the eggs of holometabolous insects remain unfertilized; in this view, it is lack of Pneuma that leaves the eggs of holometabolous insects 'imperfect' (i.e. lacking the capacity to go on to form the 'perfect' or 'complete' animal). This supposedly imperfect condition, he argues, requires them to undertake a life history that involves a period of growth and resource acquisition that only later enables them to transform autonomously into a perfect or complete pupa and then into an adult. For Aristotle, the generation of insect larvae is the same thing as spontaneous generation.

The question of spontaneous generation is central to the theme of this paper because Aristotle now goes on, as a direct result of his belief that many insects are generated spontaneously, explicitly to hypothesize a general connection between complete metamorphosis and the presumed absence of previous fertilization at the onset of life. The philosopher's logical scheme is illustrated in figure 1*b*. This postulated connection is unfortunate because we can now see that the philosopher had sufficient evidence neither to confirm the absence of fertilization in the case of flies, nor to generalize this absence to other holometabolous insects.

Why did Aristotle erroneously believe that fertilization did not occur in those insects that undergo complete

metamorphosis? I suggest that it was because he wished to extend the scope of another of his ideas about development, that sexual generation involves the transfer of an organizing principle that determines the perfect or complete form of the animal in question. It was only by asserting the absence of sexual fertilization in flies and other supposedly spontaneously-generated creatures that he was able to incorporate this idea into his general scheme of generation.

Aristotle considers the event that we call 'fertilization' quite straightforwardly (he simply equates it with mating) and we need not worry that he might have meant something else by it. He is quite clear that the function of fertilization is to confer perfection, or at least the capacity to acquire this condition, on the offspring. Aristotle envisages Pneuma as being present in the semen. Although semen is material in nature, the philosopher considers the Pneuma it contains to be an immaterial substance, in some ways similar to what we would now call a 'vital principle' (but see note 37 in Peck's Introduction to his translation of *Generation of animals*); Aristotle, however, appears to use the term in a more restricted, specifically developmental way, implying not that Pneuma confers the property of life itself, but that it is something that enables development to proceed towards perfection by supplying a template that determines the general form of the resulting animal, thus allowing it to be recognized as belonging to its own species. Leroi [2, p. 90] has commented that it is interesting to say the least that Pneuma's role in specifying the form of the embryo could be regarded as supplying the information necessary for embryogenesis, in exactly the same way that paternal and maternal DNA together specify the offspring's phenotype. While we need to beware of anachronism (although Aristotle was interested in human genetics, his understanding of inheritance was at that time necessarily very limited), this is a timely reminder that teleology (in the sense of the specification of a developmental outcome before it has begun) has not completely disappeared from our current set of ideas about developmental biology.

Unfortunately for Aristotle's theory, there is in fact no connection at all between fertilization and the incidence of complete metamorphosis. It is indeed true that some insect eggs are able to develop without fertilization (see above), but Aristotle is unlikely to have encountered this. Given that he equated fertilization with mating, Aristotle's error is surprising. In *Generation of animals* the philosopher states clearly that although he has observed insects mating, he does not believe that this activity is what it appears to be, because he does not believe that this act results in fertilization. As a result, in some cases he simply denies that mating takes place at all, even though he says elsewhere that he has seen it to occur. For example, he says:

> Other [insects] although they copulate and generate, generate not creatures of the same kind as themselves but only larvae, and these insects moreover are not produced out of animals nor do they copulate; such are gnats, mosquitoes, and many similar kinds of insects. [4] [GA 721a7-13]

Alternatively, he explains the problem away by asserting that although in other cases copulation does indeed take place, no semen is transferred during the mating (even though he could not have known whether this was true). For example, he says:

> The natural practice of those animals that emit no semen is to remain united for a long time, until [the male] has 'set' the fetation: those insects which copulate are an example of this. [4] [GA 731a 15-18]

Aristotle is obliged to take this position simply because of his belief that the purpose of fertilization is to confer Pneuma on the offspring of the union, and he has already decided that, in these animals, their later metamorphosis is evidence of their lack of Pneuma. But the problem now arises that there has to be a *cause* (above all, Aristotle believes in causes) for the initiation of development in these supposedly unfertilized eggs. Referring to those insects that mate, but which he believes transfer no semen, the philosopher now asserts that Pneuma acts at a distance, Nature itself intervening to initiate (spontaneous) generation:

> in the case of these insects [i.e. those that transfer no semen], the same effect [as is caused by semen] is produced by the heat and *dynamis* inside the [male] animal itself. [4] [GA 729b29-31]

> males of this sort are so weak that Nature is unable to accomplish anything at all through intermediaries… their movements are only just strong enough when Nature herself sits watching over the business; the result is that here Nature resembles a modeller in clay rather than a carpenter; she does not rely upon contact exerted at second hand when fashioning the object which is being given shape, but uses the parts of her very own self to handle it. [4] [GA 730b28-32]

11. Aristotle: metamorphosis and the resources available in the egg and larva

Aristotle's error concerning fertilization is important, because it leads him to suggest that a holometabolous larva is unable to develop directly to adult form because the insect

> deposits the eggs as it were before their time, which suggests that the larva, while it is yet in growth is a soft egg. [4] [GA 758b19-22]

He supposes that because it lacks Pneuma, the egg and the embryo it contains are unable to develop to perfection (i.e. are unable to reach 'the right time'). To correct this lack of Pneuma, the imperfect offspring must first undergo two distinct stages of growth and development before it can attain the perfect, complete form of the pupa-egg, which is only then able to generate an adult individual. In other words, it is because of the lack of Pneuma that metamorphosis is necessary (figure 1*a*).

It is at this point in his argument that the philosopher appears to confuse the material and information-containing qualities of the developing insect. He says that because it is unfertilized, a holometabolous insect egg lacks the necessary resources to attain perfection, which must instead be acquired from some other source than the male parent. To do this, the egg hatches to an imperfect larval form, which:

> does grow and takes nourishment, until its differentiation is effected and it has become a perfect egg. [4] [GA 758b34-36]

The 'perfect egg' that Aristotle is referring to here is the pupa. But from whence is the necessary Pneuma acquired? Here is yet another link between Aristotle's ideas about spontaneous generation and metamorphosis. Effectively the philosopher is saying that spontaneous generation is merely the acquisition by an animal of the capacity to proceed in development. The result will be the same whether this capacity is acquired through fertilization prior to the first (embryonic) metamorphosis, as in hemimetabolous insects, or from some unknown internal or environmental source prior to the second (pupal) metamorphosis, as in holometabolous insects.

But this causes yet another problem. Aristotle is now apparently supposing that the missing Pneuma is a material resource of some sort, for which some other substance present in the larva's food (or at least manufactured from it) can be substituted. This supposition does not fit with the idea presented elsewhere in *Generation of animals* that Pneuma is not a material resource; moreover, since in this case Pneuma can evidently be acquired by both male and female larvae, it also does not explain why in hemimetabolous insects (just as is the case in sanguineous animals), Pneuma can be supplied only by the father. The philosopher does not seem to notice that he has previously asserted that it is only the female that contributes material to the egg, and that the male's contribution to generation is limited to that of specifying form. (This is, of course, a quibble: today we see no problem in allowing that the informational content of the male's contribution to the offspring is in fact embodied in the material substance DNA.)

12. Aristotle: the problem of honeybees

Aristotle comes up against a particularly puzzling problem with honeybees, insects that he evidently studied in considerable detail himself as well as consulting professional beekeepers. He says 'The generation of bees is a great puzzle' [4] [GA 759a8]. The problem is as follows. He recognizes that bees have three separate castes (he does not correctly interpret the reproductive roles of these castes, thinking that queens are actually 'leaders' or 'kings', and he is also uncertain as to the sex of drones; but this is not the problem addressed here). First, Aristotle addresses the issue of whether bees are the result of spontaneous generation. To be consistent, this should be his conclusion, since bees are clearly members of the Holometabola. The philosopher considers among some other fantastic possibilities, that bees might actually 'fetch their offspring from elsewhere…' these having 'sprung into being spontaneously or [having] been produced by some other animal' [4] [GA 759a10-14]. He rejects these possibilities and says that bees must copulate (even though he says that 'none of them has ever been seen in the act of copulation' [4] [GA 759a20-25]); he concludes that they must mate to produce their own offspring, but then recognizes that this causes its own problem, which is that one of the following three options must be true:

> (i) each kind generates its own kind, or (ii) one of the three kinds generates the others, or (iii) one kind unites with another kind. [4] [GA 759a16-18]

Aristotle now seems to despair, concluding that 'all of these theories are impossible' [4] [GA 759a25]. The first option is ruled out by the fact that each caste is clearly a single sex. Among the arguments advanced to show that the other two theories are unreasonable, he points out that if bees are not generated by their own kind, then surely there would be no reason for bees altruistically to nurture offspring that are not their own:

> All creatures which concern themselves about young ones take that trouble over what appears to them to be their own proper offspring [4] [GA 759a36–759b2]

It is evident that neither Aristotle nor his beekeeper informants know the answer to the question of how bee social life and sexual reproduction are organized (this is not surprising since (i) queen bees copulate on the wing to acquire semen, and (ii) in any case produce the worker caste by means of parthenogenesis and reproduce sexually using internally stored sperm). In the end the philosopher decides that copulation probably does occur in bees (the reason for this decision is not properly explained, but it is pertinent that Aristotle notes that copulation can readily be observed in vespid wasps and hornets, and these are similar kinds of insects to bees).

The philosopher now has a problem. Surely if bees do copulate then they should belong to that category of insects which he has elsewhere asserted produce perfect offspring? But Aristotle correctly notes that although bees (and other social hymenopterans) copulate, they nonetheless produce obviously imperfect offspring in the form of larvae, which follow a typical holometabolan life history:

> The same sequence of development is followed by other insects which arise out of larvae, both those larvae which arise as the result of copulation of living animals and those which arise without copulation. Thus: the larvae of bees, anthrenas and wasps, while they are young take nourishment and are clearly seen to have excrement; but when they have passed from the larva stage to their clearly-defined stage—being then called pupae—they take no nourishment and have no excrement; they remain stationary, shut up inside, until their growth is complete, and then they break the covering with which the cell is sealed and make their way out. [5] [HA 551a28–551b6]

He does not address this problem except by asserting that some kinds of mating are not actually mating at all. Perhaps, not all of the offspring are generated in the same way? Aristotle correctly deduces that the 'kings' or 'leaders' (actually queens) generate both their own kind and also the ordinary 'bees' (i.e. workers), and even that drones are generated without copulation (although he incorrectly assumes that it is the workers that produce them). Having got so close to the right answer it seems disappointing that Aristotle fails to recognize that the drones are male and that it is they that mate with the female leader (queen). He concludes (wrongly) that the drones do not reproduce at all.

He constructs a scheme that allows the leaders to generate their own kind by means of sex, and to produce other kinds of bees as offspring without mating but concedes that he has no evidence for this.

> We see then that the manner in which bees are generated appears to be peculiar, in keeping with their extraordinary and peculiar character… The reason is that the 'bees themselves' [workers] are not generated in the same way as flies and other such creatures, but from a kind which though different is akin to them—they are, of course, generated from the 'leaders'. [4] [GA 760a5-13]

But then he is faced by yet another difficulty: if bees do generate offspring through copulation, then according to the philosopher's own theory of generation, they should generate their own kind (i.e. caste), not a different kind of offspring. Here he is handicapped by failing to realize that the 'leaders' are actually female queens. Since in Aristotle's scheme of generation the form of the offspring is determined by male Pneuma, he could have argued that the form (caste) of the offspring produced by mating with a male bee could have been determined according to whether the queen was mated or not.

Eventually the philosopher gives up the effort to integrate the sexual life of bees with that of any other animal and concludes that they are in a class of their own. He says:

> This then appears to be the state of affairs with regard to the generation of bees, so far as theory can take us, supplemented by what are thought to be the facts about their behaviour. But the facts have not been sufficiently ascertained, and if at any future time they are ascertained, then credence must be given to the direct evidence of the senses more than to theories. [4] [GA 760b28-33]

13. Aristotle: both epigenesis and preformation

As Devin Henry has pointed out [19], the autonomous development of a new animal from the material of an apparently formless egg can only be a source of wonder, whether considered from the point of view of an ancient Greek, a seventeenth century physician, or even a present-day citizen.

Rejecting magic or miracles, two obvious explanations for such an astounding event are available: the first, essentially teleological idea of *preformation* is that the morphogenetic process requires a pre-existing template that imposes form on the materials of the developing embryo (i.e. morphogenesis is the result of preformation); the alternative, apparently mechanistic explanation of *epigenesis* is that morphogenesis is the result of untutored interactions between the materials of which the embryo is composed (i.e. the formation of the offspring is due to spontaneous self-assembly from its material parts). These two contrasting ideas about embryonic morphogenesis competed for scientific approval during much of the eighteenth and nineteenth centuries [8].

Aristotle is frequently represented as an early supporter of epigenesis (for example, Peck asserts in a footnote on p. 144 of *Generation of animals* that 'Aristotle was an epigeneticist'). Unfortunately, it is all too easy to attribute modern understanding to ancient authors, giving later meaning to their language that was not intended, nor even understood at the time; the meanings of the terms epigenesis and preformation have changed almost continuously ever since they were first used, and it is risky to recruit antique authors to modern arguments [39]. And in fact, Aristotle's position on the question of epigenesis or preformation is never clearly stated [40]. The philosopher is uncharacteristically modest in confessing his inability to explain what is going on, saying:

> And on this subject we are confronted by no small puzzle. [4] [GA 733b23-24]

However, we may glimpse Aristotle's probable view in his long and detailed consideration of the possible mechanisms whereby embryogenesis might take place [4] [GA 733b24–735a29]. The discussion is not of course conducted in the terms that are now familiar to biological scientists, of DNA, RNA and proteins; instead, the philosopher largely makes use of logic and analogy. Strongly implying that he has seen this for himself, he begins by correctly asserting that 'our senses plainly tell us' [4] [GA 734a22] that the structures of the embryo are not formed all at once but appear successively.

Aristotle next considers the possibilities that these successive developmental events might all be initiated by a single initial causal factor but nevertheless appear sequentially, or that the various developmental events might each initiate the next (i.e. one thing leads to another). Aristotle's discussion of the automaton analogy (see §2 above) makes it clear that he envisages both an original impetus (which we may interpret as a preformationist idea) and a subsequent self-organizing process (epigenesis). He also follows this position when describing the events of development in a hen's egg, in which (for example) embryonic anatomical structures appear serially in time and without apparent precedent within a formless matrix; in this he is clearly an epigeneticist; on the other hand, when considering the nature of the contribution made to the offspring by male fertilization, he appears a preformationist, since the role of Pneuma is to supply a template that specifically confers certain attributes of the perfect (adult) creature. On the other hand, Aristotle also appears to reject preformationism, in the sense of transferring an actual preformed template from generation to generation. This template is not a permanent entity, he says, and until it is needed it exists only in potential form. He says:

> It is clear by now that there is something which fashions the parts of the embryo, but that this agent is not by way of being a definite individual thing, nor is it present in the semen as something that is already perfected to begin with. [4] [GA 734b17-19]

> We have now determined in what sense fetations and semen have Soul and in what sense they have not. They have Soul potentially, but not in actuality. [4] [GA 737a17-18]

Aristotle's position is thus probably best represented by saying that morphogenesis takes place gradually through a process of internal change within the material of the egg or pupa, and that this developmental process is shaped by an externally supplied template newly formed in the embryo through the action of Pneuma. Despite the implication that the developmental process is at least mechanically epigenetic, it cannot be denied that Aristotle does indeed envisage a supervisory teleological role for the template, once it has been formed.

14. Aristotle reloaded: William Harvey

Although the English court physician and anatomist William Harvey (1578–1657), famous as the discoverer through experiment of the circulation of the blood, claimed that his scientific knowledge came 'not from positions of philosophers but from the fabric of nature', he was also a keen student of Aristotle's writings [41] and late in life (in 1651) he published a study of animal reproduction and development, *Exercitationes de generatione animalium*, that was heavily influenced by his classical Greek predecessor. Harvey's essential idea on morphogenesis was expressed in the motto '*Ex ovo omnia*' (from the egg, all) [9].[6] This work drew on Harvey's experience as a medical practitioner as well as his dissections of developing hens' eggs and pregnant deer from the King's estates. But in it, Harvey also made a number of influential observations on the reproduction, development and metamorphosis of insects. Like Aristotle, Harvey was aware that it is much easier to study the process of morphogenesis in an insect pupa than in the eggs of birds or mammals.

15. Harvey: perfect and imperfect eggs

Harvey's main ideas about spontaneous generation, fertilization and metamorphosis [9] are in many ways very similar to those of Aristotle. The main difference between them is that Harvey insists that animals can only develop from eggs, and this must be true of insects too. This was in many ways an act of faith, since like Aristotle, Harvey could not actually see the eggs of mammals and other viviparous animals. As a consequence of this, Harvey's definition of an

egg is so plastic that it is hard to pin him down on just what he means by it. Basically, he says that an egg is some material substance from which an animal emerges. Thus, an egg may not look like an egg; an assertion of which he makes considerable use when considering insect complete metamorphosis.

Importantly, however, one of Aristotle's central notions about development retained unchanged by Harvey is the idea of the perfect state. Thus, like Aristotle, Harvey asserts that the larva that hatches from the egg of a holometabolous insect is imperfect; it must feed and grow in order to attain perfection, and until it does so it is unable to generate another adult insect. He says:

> Imperfect eggs we call those which are thrust out while they are immature and have not yet reached their full size but continue to grow outside the womb after they have been laid. …in this class also should be included the primordia of insects, which Aristotle calls worms, and of those creatures which arise spontaneously. [9, p. 327]

Harvey is explicit in saying (i) that the egg that generates an imperfect larva is not a proper egg, and as such should not be called an egg; (ii) that perfection is only attained at the end of larval life, and that it is this that enables the metamorphosis of the larva to the 'perfect egg' of the pupal state. This is what he says:

> So also among imperfect eggs, those are rightly so called from which a perfect animal is created, for example, the eggs of a fish, while others [i.e. eggs] from which an imperfect animal proceeds that is a worm or a caterpillar, are improperly so named. These are a kind of intermediary between a perfect and an imperfect egg, because in comparison with its own egg or primordium, it is an animal endowed with sense and motion that nourishes itself, but in comparison with the fly or butterfly whose primordium exists in it *in potentia*, it is to be accounted no more than a crawling egg, itself providing for its own growth. Such is a caterpillar which, having acquired its proper size, is changed into a chrysalis or a perfected egg, and ceasing to move is, like an egg, an animal *in potentia*. [9, p. 327]

Harvey follows Aristotle's ideas on fertilization and metamorphosis, being quite explicit in saying that the holometabolous insect egg is not originally fertilized by a male parent; moreover, since no subsequent fertilization of either the larva or the pupa takes place, he concludes that fertilization is unnecessary for the development of the perfect adult insect.

Why did Harvey go to such trouble to deny the egg-nature of a holometabolous insect egg? I suggest that it can only be because he could not exclude the possibility of spontaneous generation, which ever since Aristotle had been generally supposed to account for the generation of such insects.

16. Harvey: spontaneous generation

Thus, Harvey is obliged by his own logic to suppose that holometabolous insects do not undertake sexual reproduction. Just as was the case for Aristotle 2000 years previously, Harvey is forced to deny the reality of what he has himself seen by saying:

> But some of these spontaneously developed creatures, although they copulate in appearance, either do not beget or else they beget only some other thing… just as out of some caterpillars are created butterflies. [43, p. 179]

[This passage is quoted verbatim in section 5 of the Introduction to [9]]

Thus, because Harvey believes against the evidence of his own eyes that holometabolous insects do not reproduce sexually, he is like Aristotle driven to propose the existence of a spontaneously generated transforming principle.

Exactly what Harvey meant by 'spontaneous' in this context is unclear and has been the subject of debate ever since his book was published. It is evident that Harvey considers two different types of spontaneity. The first is that which permits an imperfect egg 'univocally' (a word used here by Harvey specifically to mean without change in form) to generate an imperfect larva; following Aristotle, Harvey assumes that this kind of generation is independent of fertilization. Even if mating appears to take place, he thinks that there is no reason to suppose that it leads to fertilization.

Harvey's second type of spontaneity is the 'equivocal' transformation of the pupa into an adult insect ('equivocal' is a term here used by Harvey to mean that it involves a change of bodily form). Since no post-embryonic mating occurs prior to adulthood, this transformative generation must again necessarily be 'spontaneous'. Indeed, Harvey more than once characterizes all insects as *sponte nascentia* (spontaneously generated), even though he must have recognized that many insects do not follow the complete metamorphosis life-history pattern that he is talking about. In this, Harvey appears less of an entomologist than Aristotle.

This question of whether Harvey believed in spontaneous generation from inanimate material as it is now generally understood has been carefully examined [44]. Although today we may find Harvey's remarks about spontaneous generation to be unduly cautious, possibly even actually supportive of its spontaneity (through his failure to deny it), Harvey's own contemporaries may have found his lukewarm words on the subject to be just the opposite; the publication of *De generatione* appears to have led to a rapid change in general opinion (belief in spontaneous generation having been essentially universal prior to Harvey) that quickly led other scientists to devise their own experimental tests of the question.

Although the by now elderly Harvey (who had made his name as an experimental physiologist) himself conspicuously failed to do any experiments, less than 20 years later the younger Italian scientist Francesco Redi (1668) interrogated the idea of spontaneous generation with a practical test [34,45]. Only 17 years after the publication of Harvey's book, Redi found by covering a vessel with a cloth that fly larvae are not generated on putrefying matter unless adult flies are allowed access. Famously, this was among the first scientific experiments to include a proper control, in which the covering cloth was omitted from a similar carcass. When reporting his own results, of course, Redi was keen to draw attention to the fact that in *De generatione* Harvey had been reluctant to state that spontaneous generation did *not* occur. Thus, he was able to represent his own paper as a refutation of Harvey's position [8]. Having said this, though, although Redi's experiment conclusively showed that flies are not spontaneously generated within an animal carcass, it took more than another 100 years before a general disproof of spontaneous generation in other organisms was accomplished [8,34,45].

17. Harvey: epigenesis versus metamorphosis

Harvey has frequently been credited with advancing beyond Aristotle in considering the question of whether morphogenesis, either in the egg or in the pupa, is due to an epigenetic

process. We have already seen that Aristotle himself did not think that it was possible to separate the mechanics of development from its teleological purpose. The matter is of some interest because of the extended argument that subsequently took place in the eighteenth and nineteenth centuries about preformation, a debate that also incorporated ideas about free will and predestination [46]. Simply stated, 'preformation' is the idea that the morphogenetic process requires some form of pre-existing template to impose form on the material undergoing development.

The problem with preformationism is that, in tracing back the source of this preformed template, it is difficult to know where to stop; is the template created anew in each generation (in which case the idea has little to recommend it over epigenesis)? Or has the template always existed, having been passed unchanged through successive generations ever since the Creation? Preformationism in the latter sense did not long survive the discovery of the laws of genetics and the development of evolutionary theory [8,42]. But even before that, the debate over preformation drew on observations of the complete metamorphosis of insects.

Harvey does use the word epigenesis, and indeed he probably invented it. But his conception of the mechanism of epigenesis and its significance in generation was very different from that of many of those who followed him. Whereas today we might consider that to display epigenesis the development of the embryo (or pupa) should be a process that occurs through some kind of self-organization, specifically without the benefit of a previously supplied exogenous template (i.e. it is not due to preformation), Harvey simply asserted that development is epigenetic in nature if it involves gradual processes of growth and acquisition of nutrients derived from outside of the larva itself; it is these materials that are converted by the egg itself into material of perfect form, this perfection being acquired gradually rather than all at once. Concerning the development of a hen's egg, Harvey says:

> What Aristotle says about the generation of a perfect animals is undoubtedly true and clearly to be seen in the egg, namely, that not all the parts are made simultaneously but one after the other in order, and that the first to exist is the genital particle by virtue of which all the remaining parts do later arise as from their first original… And because no part begets itself, but after it is begotten, increases itself, so that part must needs be made first which contains the principle of increase… At the same time that part divides up and forms all the other parts in their due order. Therefore, in that same first begotten particle there is present from the beginning the soul, the author and principle of sensation and movement and of the life of the whole. [9, p. 240]

Like Aristotle, Harvey likens the process by which perfection is acquired to cooking (both of them took for granted that a supply of energy was something to do with the morphogenetic process). But unlike Aristotle, Harvey asserted that the transformation of an insect pupa to an adult is not epigenetic, because it occurs all at once, and involves no growth in size.

Interestingly, in the light of the subsequent 200 year debate as to whether morphogenesis is due to epigenesis or preformation, Harvey does not in *De generatione* use the term preformation at all. Instead, he simply opposes epigenesis to metamorphosis. It has been suggested [46] that for Harvey there is a difference between metamorphosis and preformation, in the sense that he meant the term metamorphosis to apply only to non-sanguineous animals (i.e. mostly insects). It seems to me, however, that Harvey must have been well aware that his use of the term metamorphosis would be useful beyond just insects. It is worth setting out exactly what he says:

> Some animals are formed out of material that is already concocted and grown, and are transfigured, and all their separate parts arise at the same time by a metamorphosis, and a perfect animal is born. Some have their parts made one after another, and then, out of the same material they are at the same time nourished, increased and formed before the others which are formed later… Now the construction of these begins from some one part as from its original, and by its help the other members are produced, and these we say are made by epigenesis. [9, p. 202]

It is in these terms that Harvey asserts that the first transformation undertaken by a holometabolous insect, in which the imperfect egg hatches to form an imperfect larva and subsequently increases greatly in size without significant change in morphology, is achieved through epigenesis, while he considers that the second transformation, in which the fully grown larva is transformed first into a pupa and then an adult, is achieved through what he calls metamorphosis. In other words, according to Harvey, epigenetic development is epigenetic simply because it is not metamorphic.

But in my opinion Harvey goes further than this, adopting a position that may with justification be called preformationist, when he says of metamorphosis:

> In generation by metamorphosis creatures are fashioned as it were by the imprint of a seal, or cast in a mould, that is the whole of the material being transformed. But an animal which is procreated by epigenesis draws in the material and at the same time prepares and concocts and uses it; at the same time that the material is formed, it grows…. From the homogeneous material it makes that which is heterogeneous, that is to say, out of the homogeneous material that is submitted to it, it makes organs that are heterogeneous. [9, pp. 203–204]

I have previously noted that the position taken by Aristotle on epigenesis or preformation was non-committal. Harvey is here following the Greek philosopher in saying that the difference between an egg and a larva is that while an egg uses only a part of its resources to nourish the larva within it, the whole of the larva is consumed in the production of the pupa and then of the adult [4] [GA 732a30-32]; the difference is that Harvey is using this fact to justify his statement that pupal–adult development is not epigenetic—Aristotle had said no such thing. Although the philosopher never used the term epigenesis or anything like it, Aristotle (unlike Harvey) evidently did not consider epigenesis to be the opposite of metamorphosis.

Why did Harvey differ from Aristotle on this point? Perhaps he had justifiable scientific concerns about whether it was possible to prove that epigenesis, in the sense of uninstructed autonomous self-assembly, can occur at all. He did not discuss the point, but he may have been aware that to accept this kind of epigenesis as the sole explanation of animal (and implicitly human) development would require proof of the absence of a developmental template. To prove its absence would be difficult or even impossible unless he had certain knowledge of what such a template would look like, which of course he did not.

Although it is not stated very clearly, it appears from *De generatione* that like Aristotle, Harvey thought that the material content of the pupa is egglike and formless. He could only have thought this if he did not look very carefully at it. It would not have been necessary to use a microscope to

discover that the pupal shell encloses what is obviously a developing adult insect right from the time at which it moulted from the final larval stage. The first person to say this in print (in 1669) was Marcello Malpighi [10], who stated that he had seen adultiform structures such as the wings and other appendages concealed under the cover of the late larval cuticle 'even before the cocoon is spun', and also in the pupa. Jan Swammerdam, who we now know had already seen the same thing [47], responded in the same year by publishing similar observations [8, p. 152; 11]. We would now say that Malpighi and Swammerdam were looking not at the larva at all, but at the pharate pupa, a stage in between larval-pupal apolysis and pupal ecdysis, which pupa is still enclosed by the old larval cuticle [48]. Although Swammerdam dedicated his book on silkworm anatomy and development to Harvey, in the text he condemned Harvey strongly for failing to examine the inside of the pupa properly. Nevertheless, Harvey deserves great credit for stimulating renewed interest in complete metamorphosis [49].

It is unfortunate that Harvey's own extensive notes on insect reproduction and development were destroyed during the English Civil War (1642–1651) so that the entomological content of *De generatione* was in the end much less detailed than its author had intended [9, p. 354]. We cannot rule out the possibility that Harvey did indeed examine the inside of an insect pupa, and that he was aware that the inside was not formless, but nothing in *De generatione* suggests this.

18. Aristotle's legacy: neoteny, recapitulation, transcription factors and evo–devo

Aristotle's (and Harvey's) way of thinking about reproduction and development (especially its vocabulary) does not always make comfortable reading for a twenty-first century biologist. In relation to metamorphosis, the philosopher's ideas about spontaneous generation, and the supposed lack of fertilization in holometabolous insects are just wrong. But Aristotle's legacy nevertheless continues to influence current thinking about metamorphosis, even if we do not always recognize the footprints of the philosopher on our own ideas.

We do not know how the morphology and life history of the ancestral holometabolan differed from its hemimetabolous precursor, nor what selective forces acted to cause its divergence from that condition [50]. In this respect, Aristotle's opinions are still interesting. In particular, the philosopher's idea that the larvae of insects undergoing complete metamorphosis are, as he put it, 'born too soon', and that this accounts for their simpler body plan when compared with the nymphs of hemimetabolous insects, has endured for over 2000 years. The idea that we can learn about phylogeny from studying embryos has had an up-and-down history from about 1800, with the introduction of the idea of developmental recapitulation, to Haeckel's Biogenic Law of the mid nineteenth century, and eventually the grudging acceptance in 1922 by Garstang [51] of a modified principle of embryonic recapitulation. Today, the emphasis in considering how embryonic and larval development influence are influenced by evolution is on the modulation of developmental timing or heterochrony, as was first suggested in 1930 by de Beer [52]. The history of these ideas is well told by Gould [22].

Aristotle's basic idea (adopted without change by Harvey) about the complete metamorphosis of insects was that, in preparing to hatch from the egg, the embryo of such insects develops heterochronously; instead of developing to an adult-like form as hemimetabolous insects do, a holometabolous embryo fails to progress towards perfection and thus retains a neotenous embryo-like form when it hatches. This is the larva, which has a typically 'primitive' morphology, quite unlike the adult it is destined eventually to become. Many adaptive benefits can now be proposed to result from this developmental delay, which range from a faster rate of feeding and growth to enhanced defensive capacity [50]. This is what Aristotle actually says:

> The fifth class of creatures, which are the coldest of all, do not even lay an egg directly themselves, but the formation of their egg takes place outside the parent… What happens is that insects first produce a larva, then the larva develops till it becomes egg-like…. [4] [GA 733b13-15]

In proposing this idea, Aristotle thought that the reason for the prolongation of the embryonic condition into larval life was the result of its being generated without parental fertilization, and in consequence suffering from a lack of Pneuma. In turn, absence of Pneuma meant that the developing insect was imperfect or incomplete and was therefore unqualified to progress to a 'higher' level of development (I have already discussed what 'higher' means).

In modern terms, the idea that complete metamorphosis is linked to the absence of fertilization is just wrong. But Aristotle's concept of a requirement for Pneuma to enable morphogenesis to progress is much closer to modern understanding. Although the philosopher conceived Pneuma to be an immaterial substance that enables development to continue towards the perfect state, Pneuma may nevertheless be regarded in modern terms as equivalent to an enabling signal within the embryo, which licenses an existing developmental programme to progress. Further discussion of the possible involvement of Pneuma-like factors in the evolution of complete metamorphosis would be unwise, partly because Aristotle's ideas were formed in a completely different intellectual context, but also because present-day molecular understanding of insect development remains incomplete and is limited to just a few species; moreover, after 350 Myr the role of any such factor in present-day insects is in any case unlikely to be the same as it was in the insect that underwent complete metamorphosis for the first time.

Following Aristotle, but in general not acknowledging their debt to the ancient philosopher, several entomologists have proposed theories to explain the evolutionary origin of the holometabolous larval stage that are based on heterochronic expression of developmental factors that regulate progression from the imperfect to the perfect condition; they include Lubbock [53], Berlese [54], Imms [55], Williams [56] and Truman & Riddiford [57–59]. Like Aristotle and Harvey, all of these theories suppose that the larva is 'born too soon' in a condition which is developmentally immature only in the sense that some developmental pathways that would normally be activated at an earlier stage have not yet been recruited. It is not necessary to suppose that the larva is literally a delayed embryo. Moreover, as pointed out by both Lubbock [53] and Williams [56], one would not expect that present-day- insect larvae and pupae would have spent the 350 Myr period since the origin of holometaboly uninfluenced in form by selective pressures.

In this special issue, other papers by Bellés [60] and Ishimaru *et al*. [61] Jindra [62] each discuss alternative theories for the origin of the pupa; these are derived from the idea of Hinton [63], which supposes that the pupal stage arose as a modified final larval stage. But even here, we can recognize the unacknowledged debt to Aristotle, because the basic idea is one of the modulation in time of the sequence of developmental change. Here, the characteristics of the pupal stage might be explained by supposing that some (but not all) aspects of adult form might be recruited heterochronously in the last preadult stage, resulting in the production of an external body shape that is intermediate between the ancestral adult and larval forms. This would explain why the pupa prematurely displays many external (cuticular) features that are similar to but less well-developed than those of the adult (e.g. well-developed appendages), while the expression of other typically adult features (e.g. reproductive organs) is delayed until the true adult stage. Such a scheme is not enough to 'explain' the pupa as we know it, since there are also other aspects of the pupal phenotype (cessation of feeding, extensive reorganization of internal organs etc.) that are specific to the pupal stage, but might be secondary to the original heterochrony.

19. Conclusion

Many (although admittedly not all) of Aristotle's contributions to biology, developmental biology in particular, were astonishingly penetrating considering that they were made almost 2500 years ago [1–3]. I hope that in this paper I have managed to highlight the significant role that the philosopher's examination of the complete metamorphosis of insects played in the development of his thought concerning morphogenesis. There is no doubt that his impact on our understanding of metamorphosis was great, not least because his ideas were the starting point for the much later work of Harvey, Malpighi and Swammerdam.

Even when Aristotle's influence has not been recognized by those in his debt, we continue to subscribe to his basic idea that most of animal development can be ascribed to a combination of a pre-programmed sequence of morphogenetic change that progresses stepwise towards a genetically defined (in Aristotle's terms, 'perfect') endpoint, and a process of epigenetic development that realizes the potential that is inherent in the material components of the egg.

On the other hand, we no longer think, as Aristotle and Harvey did, that an insect pupa is similar to an egg. Moreover, our modern understanding that 'spontaneous generation' does not occur in nature has freed us from the need of those early writers to explain complete metamorphosis as a consequence of such spontaneity.

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Endnotes

[1]All quotes from Aristotle are from the Loeb parallel Greek–English editions of 'Generation of Animals' [4] or 'History of Animals' [5,6]. References to the Greek text are given as Bekker numbers in the standard format of Aristotelian scholarship. Full bibliographic details of the editions that I have consulted are in the reference list.

[2]There is a detailed discussion of Pneuma etc. by the translator, A. L. Peck, in Appendix B of [4].

[3]This way of looking at the morphogenesis of offspring arises from Aristotle's general theory of causation; there is a good discussion of this in Peck's Appendix B in his translation of *Generation of animals* [4]. In these terms, the organizing principle supplied by the male parent is an efficient cause; the material that is organized, which is supplied by the female parent, is the material cause; and the essential characteristics, or Perfect form of the developing animal is the formal cause.

[4]Aristotle's error in the case of wasps and ants is curious, since he specifically refers to the generation of wasp larvae in [6] [HA 628a16-22]. The error may arise from the fact that both these insects emerge from oviform pupae, which he may either have mistaken for actual eggs, or have considered to be equivalent to eggs, despite the fact that they arise from a previous larval stage.

[5]The translator (Peck) comments that what Aristotle literally says is 'has the dynamis of an egg' [4].

[6]These words appeared in the frontispiece illustration to Harvey's book, and it is uncertain whether he in fact wrote them himself, although they well summarize the content of the book. See the discussion in [42].

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