Evo-devo: A New Evolutionary Paradigm?[1]

MICHAEL RUSE

> The homologies of process within morphogenetic fields provide some of the best evidence for evolution—just as skeletal and organ homologies did earlier. Thus, the evidence for evolution is better than ever. The role of natural selection in evolution, however, is seen to play less an important role. It is merely a filter for unsuccessful morphologies generated by development. Population genetics is destined to change if it is not to become as irrelevant to evolution as Newtonian mechanics is to contemporary physics. (Gilbert, Opitz, and Raff 1996, 368)

These are exciting days for evolutionary biology. In the past twenty years or so, the molecular approach to biology—evolutionary development or more familiarly 'evo-devo'—has swept all before it. Now we can trace development from the gene to the finished organism. Along the way, some magnificent discoveries have been made, most significantly that organisms as different as the fruitfly and the human share hugely important genes for development. We humans are put together in the same way as are those little insects that hang around compost heaps and rotting vegetables in garbage cans. This has led some enthusiasts to think that we are on the verge of—certainly in need of—a whole new theory of evolution. A new paradigm, that rejects Darwinian natural selection, or that at least reduces it to an unimportant role in cleaning up after the real work has been done. Now we have or are after a new theory—perhaps one that makes the really creative work appear in the course of development. Nature unfurls according to its molecularly based developmental laws, and that is where the real sources of change should be sought. It is true that the fittest survive, but this is little more than a truism with no real evolutionary import.

I am not sure that this is so. I applaud the new work in evo-devo—I think it is some of the most exciting that has ever been done by evolutionists. But whether this spells the demise of natural selection—the end of Darwinian evolutionary theory as we know

[1] Much of the discussion in this essay is based on the relevant parts of my recent book, *Darwin and Design: Does Evolution have a Purpose?*

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it—is altogether another matter. I think, in fact, we are seeing an ongoing debate that dates back to Aristotle, between what biologists have labelled 'form' and 'function.' The debate predates the coming of evolution, and it postdates it also (Russell 1916; Ruse 1989). Which has interesting consequences for those of us trying, as philosophers, to understand the nature of science. In a way, I do think we have different paradigms, but unlike the normal understanding of 'paradigm,' I am not sure that one is replacing—will ever replace—the other. This is something that biologists should realize and philosophers should try to understand. Which is why I am writing this essay.

Form and function

We have two ways of looking at organisms. It is useful and illuminating to speak of them as two different paradigms, because there is overlap with what is going on in biology with the usage of that term by Thomas Kuhn in his *Structure of Scientific Revolutions* (1962), although I admit fully that there are differences from his usage. For Kuhn, a paradigm is a way of looking at things—now you see it one way, now you see it another. Now you see the earth stationary and everything going around it; now you see the sun stationary and everything going around it. This is not just a question of reason but more a question of attitude. From taking one or the other position, a whole discipline can be founded, with its own research problems or puzzles and its own techniques and much more.

It is in this sense, in this essay, that I use the word 'paradigm.' In the world of organisms, you either see function as dominant—as all-pervasive—and everything else as secondary, or you do not. If you do not, then various formal structures and so forth are what dominate your thinking. If you are a functionalist, then your job is to find function and explain it. If you are a formalist, then your job is to find structure and explain it. Differing from a Kuhnian paradigm, no one is exactly and exclusively a subscriber to the one position and not to the other—although some people get pretty close to the extremes—and these positions and commitments are ongoing. As noted, the psychological picture—the way of seeing—is what is central to a Kuhnian paradigm, and it is this which is central to the way in which I am using 'paradigm' here. Some see function, and form is secondary and virtually a nuisance, and some see form, and function is secondary and virtually a nascence.

Aristotle, a first-class biologist, spotted both senses or ways of viewing organisms. On the one hand we have function, or what today is often called teleology. What Aristotle called final cause.

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> [We have cause] in the sense of end or that for the sake of which a thing is done, e.g. health is the cause of walking about. ('Why is he walking about?' We say: 'To be healthy', and, having said that, we think we have assigned the cause.) The same is true also of all the intermediate steps which are brought about through the action of something else as means towards the end, e.g. reduction of flesh, purging, drugs, or surgical instruments are means towards health. All these things are for the sake of the end, though they differ from one another in that some are activities, others instruments. (*Physics* 194b 30–195a 1, in Barnes 1984, 1)

Aristotle chided: 'What are the forces by which the hand or the body was fashioned into its shape?' A woodcarver (speaking of a model) might say that it was made as it is by tools like an axe or an auger. But note that simply referring to the tools and their effects is not enough. One must bring in ends. The woodcarver 'must state the reasons why he struck his blow in such a way as to effect this, and for the sake of what he did so; namely, that the piece of wood should develop eventually into this or that shape.' Likewise against the physiologists, 'the true method is to state what the characters are that distinguish the animal—to explain what it is and what are its qualities—and to deal after the same fashion with its several parts; in fact, to proceed in exactly the same way as we should do, were we dealing with the form of a couch' (*Parts of Animals*, 641a 7–17, in Barnes 1984, 1, 997).

On the other hand there is form. 'Whatever parts men have in front, these parts quadrupeds have below, on the belly; and whatever parts men have behind, these parts quadrupeds have on their back' (*History of Animals*, Barnes 1984, 1, 793). In the case of organisms, the similarities or isomorphisms between the parts of very different animals—isomorphisms between parts with very different functions. Traditionally, one refers here to the forelimbs of vertebrates being the favourite example. The arm of man, the wing of bird, the front leg of horse, the flipper of whale, the paw of mole—all used for very different purposes but with similarities in their structures. There seems to be no final cause at work here. Homologies do not exist for the sake of some end. (We today use the word 'homology,' meaning similarity due to common descent. Aristotle was not an evolutionist. But, although the word was not first applied until the 1840s, for clarity we can use the term without undue anachronism.)

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Function across the evolutionary divide

The important point from our perspective is that these two ways of looking at organisms go across the evolutionary divide. There are pre-evolutionary functionalists. There are post-evolutionary functionalists. There are pre-evolutionary formalists. There are post-evolutionary formalists. To take the former, consider the famous arguments of the clergyman-naturalist John Ray (1628–1705), especially in his *Wisdom of God, Manifested in the Words of Creation* (1691, fifth edition 1709). His way of thinking is functional through and through. 'Whatever is natural, beheld through [the microscope] appears exquisitely formed, and adorned with all imaginable Elegancy and Beauty. There are such inimitable gildings in the smallest Seeds of Plants, but especially in the parts of Animals, in the Lead or Eye of a small Fry; Such accuracy, Order and Symmetry in the frame of the most minute Creatures, a Louse, for example, or a Mite, as no man were able to conceive without seeming of them.'

Everything that we humans do and produce is just crude and amateurish compared to what we find in nature. But this is not a conclusion that is then used to prove evolution. The very opposite. It is used for the argument to design. The living world was likened to a product of design. A machine implies an architect or an engineer, and so likewise inasmuch as the world of life is machine-like, it too implies a being, as much above us as the world of life is above our artifacts and creations. 'There is no greater, at least no more palpable and convincing argument of the Existence of a Deity, than the admirable Art and Wisdom that discovers itself in the Make and Constitution, the Order and Disposition, the Ends and uses of all the parts and members of this stately fabric of Heaven and Earth' (Ray 1709, 32–3).

A neat package, as the teleological way of thought in biology was tied back into the proof of the divine: the classic argument for design. 'That under one skin there should be such infinite variety of parts, variously mingled, hard with soft, fluid with fixt, solid with hollow, those in rest with those in motion:—all these so packed and thrust so close together, that there is no unnecessary vacuity in the whole body, and yet so far from clashing or interfering with one another, or hindering each others motions, that they do all help and assist mutually on the other, all concur in one general end and design' (Ray 1709, 335–6). Moreover, this is design which is of absolutely the top quality and so the same must be said of the intelligence behind it. This points to a being worthy of worship, not

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to some ethereal, local spirit before which the heathen humble themselves.

Then, on the other side of the evolutionary divide, we have Charles Darwin himself. Function is the starting point of his thinking about organisms. Take the little book on orchids, that Darwin published just after the *Origin*. There Darwin was laying out evolutionary biology as he hoped it would be done. 'I think this little book will do good to the Origin, as it will show that I have worked hard at details, and it will perhaps, serve [to] illustrate how natural History may be worked under the belief of the modification of species' (Letter to his publisher, John Murray, September 24, 1861, in Darwin 1985–, 9, 279). It is teleological through and through. The very title flags you to this fact: *On the Various Contrivances by which British and Foreign Orchids are Fertilized by Insects, and on the Good Effects of Intercrossing* (1862). It flags you also to the fact that, as with Paley, Darwin was looking at the organic world as if it were an object of design: he was taking organized end-directed complexity as the absolutely crucial key to unlocking the secrets of the living world and its attributes. Contrivances are human-made objects, which are created with an end in view. As in: 'I have invented a remarkable contrivance for shelling hot chestnuts without burning your fingers.' This was Darwin's perspective on the living world, just as it had been for Paley.

Then, when we get into the text of the orchids book, the natural theological perspective—the argument to complexity, that is—was used constantly, with great effect. Thus right at the beginning, speaking of how an orchid is fertilized, Darwin described in detail the 'complex mechanism' which causes this to happen. There are little sacks of pollen which are brushed by an insect as it pushes its way in, in search of nectar. But not just little sacks. Rather little sacks (or balls) which are going to go travelling. 'So viscid are these balls that whatever they touch they firmly stick to. Moreover the viscid matter has the peculiar chemical quality of setting, like a cement, hard and dry in a few minutes' time. As the anther-cells are open in front, when the insect withdraws its head,... one pollinium, or both, will be withdrawn, firmly cemented to the object, projecting up like horns' (Darwin 1862, 15). Then when the insect visits another plant, the pollen is transferred. But not just by chance. 'How then can the flower be fertilised? This is effected by a beautiful contrivance: though the viscid surface remains immoveably affixed, the apparently insignificant and minute disc of membrane to which the caudicle adheres is endowed with a

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remarkable power of contraction..., which causes the pollinium to sweep through about 90 degrees, always in one direction, viz., towards the apex of the proboscis..., in the course, on an average, of thirty seconds' (Darwin 1862, 16).

And so on and so forth. Right through the book, the picture was one of complexity, of adaptation, of function, of purpose. 'When we consider the unusual and perfectly-adapted length, as well as the remarkable thinness, of the caudicles of the pollinia; when we see that the anther-cells naturally open, and that the masses of pollen, from their weight, slowly fall down to the exact level of the stigmatic surface, and are there made to vibrate to and fro by the slightest breath of wind till the stigma is struck; it is impossible to doubt that these points of structure and function, which occur in no other British Orchid, are specially adapted for self-fertilisation' (Darwin 1862, 65). And: 'In many Vandeæ the caudicles are easily ruptured, and the fertilisation of the flower, as far as this point is concerned, is a simple affair; but in other cases the strength of the caudicles and the length to which they can be stretched before they break is surprising. I was at first perplexed to understand what good purpose the great strength of the caudicles and their capacity of extension could serve' (Darwin 1862, 182).

And of course, this functional perspective on nature was just what natural selection was supposed to address. Selection implies not just change but change towards adaptation, contrivance, function.

> A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase. Every being, which during its natural lifetime produces several eggs or seeds, must suffer destruction during some period of its life, and during some season or occasional year, otherwise, on the principle of geometrical increase, its numbers would quickly become so inordinately great that no country could support the product. Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life. It is the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdoms; for in this case there can be no artificial increase of food, and no prudential restraint from marriage. (Darwin 1859, 63)

And then on to natural selection:

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> Let it be borne in mind in what an endless number of strange peculiarities our domestic productions, and, in a lesser degree, those under nature, vary; and how strong the hereditary tendency is. Under domestication, it may be truly said that the whole organization becomes in some degree plastic. Let it be borne in mind how infinitely complex and close-fitting are the mutual relations of all organic beings to each other and to their physical conditions of life. Can it, then, be thought improbable, seeing that variations useful to man have undoubtedly occurred, that other variations useful in some way to each being in the great and complex battle of life, should sometimes occur in the course of thousands of generations? If such do occur, can we doubt (remembering that many more individuals are born than can possibly survive) that individuals having any advantage, however slight, over others, would have the best chance of surviving and of procreating their kind? On the other hand we may feel sure that any variation in the least degree injurious would be rigidly destroyed. This preservation of favourable variations and the rejection of injurious variations, I call Natural Selection. (pp. 80–81)

Form across the evolutionary divide

Turn to the other side, that of formalism. Pre-evolutionary formalists included German thinkers like Johann Wolfgang von Goethe, the great poet; French morphologists like Étienne Geoffroy Saint-Hilaire; as well as British thinkers (Richards 2003; Appel 1987; Ruse 1996). The classic case was Richard Owen who saw all organisms as being based on one fundamental archetype. 'What Plato would have called the 'Divine idea' on which the osseus frame of all vertebrate animals ... has been constructed' (Owen 1894, 1, 388). Post-evolutionary formalists abounded at the time of Darwin. In fact, it was the author of the *Origin* who was the odd man out. For all that he was a great critic of Richard Owen, Thomas Henry Huxley worked exclusively in terms of types. In the text book he coauthored with his student H. N. Martin, Huxley appealed to the type as he led the students through the living world group by group: mussels, snails, lobsters, frogs, and so forth (Huxley and Martin 1875). The same was true of others in Britain. The brilliant embryologist Frank Balfour (1880–1881) wrote that, with respect to the rabbit, 'there are grounds for thinking that not inconsiderable variations are likely to be met with in other species' (2, 214), but this did not stop him from using that very animal as the model when he

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discussed the mammals, saying indeed that for 'the early stages the rabbit necessarily serves as type'.

Likewise in Germany, notwithstanding his leadership of the 'Darwinismus' movement, Ernst Haeckel (1866) owed far more to Goethe and other transcendentalists than to anything in England. The same was true also of his some-time co-worker, the morphologist Carl Gegenbaur (1878). The latter wrote explicitly of 'the subordinate importance we must assign to the physiological duties [ie functions] of an organ when we are engaged in an investigation in Comparative Anatomy' (p. 4). He was open in his judgment that 'physiological value' was secondary and only to be used to avoid mistakes in comparisons. And in America we find that Louis Agassiz, student of the *Naturphilosophen* Lorenz Oken and Friedrich Schelling, arguing that 'one single idea has presided over the development of the whole class, and that all the deviations lead back to a primary plan' (Agassiz 1885, 1, 241). Unlike the teacher, Agassiz's most brilliant student, the invertebrate paleontologist Alpheus Hyatt, became an evolutionist at some point in the 1860s, a Lamarckian of some kind. Yet, so much had he absorbed his master's teachings, that from his papers no one can quite tell when Hyatt made the transition! At some important level, evolution really did not matter. And function was a positive handicap to the real work at hand (Ruse 1996).

Hyatt was not alone. Even when people thought about change, adaptation and function were downplayed. Although *Naturphilosophie* and its legacy was developmental through and through, it generated an attitude where the type rather than the end was the fundamental organizing concept. The model here, of course, is the individual organism—the very idea of evolution itself is linked to individual growth. Hence, there was a long tradition of drawing an analogy between the order in which organisms appear in the fossil record and the order of the various changes in the embryonic development of the single organism (Richards 1992). Agassiz indeed drew a three-fold parallelism, between the history of life, the history of the individual, and the order of complexity to be found across today's organisms. 'One may consider it as henceforth proved that the embryo of the fish during its development, the class of fishes as it at present exists in its numerous families, and the type of fish in its planetary history, exhibit analogous phases through which one may follow the same creative thought like a guiding thread in the study of the connection between organized beings' (Agassiz 1885, 1, 369–70).

With the coming of evolution, Haeckel (1866) converted the

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history into phylogeny—the history of the developing class—and thus he had his so-called 'biogenetic law,' that the history of life can be found in the history of the organism. 'Ontogeny recapitulates phylogeny.' In fact, morphologists themselves grew increasingly critical of this law in its crude form—there are far too many exceptions—but generally speaking, however people drew the connections between paleontology and embryology, there was little or no interest in seeing the development of the type through time as being selection-driven. Other forces, internal forces akin to the forces that lead to individual growth, were thought the key to organic history.

Constraint

As is well known, in the 1930s the world of evolution took a dramatic turn to Darwinism and function. Thanks to the work of the population geneticists like R. A. Fisher and J. B. S. Haldane in Britain and Sewall Wright in America, and then the experimentalists and empiricists like E. B. Ford in Britain and Theodosius Dobzhansky in America, natural selection was recognized as the dominant mechanism of evolutionary change and function was seen to be the dominant feature of living beings (Ruse 1996, 1999). Entirely typical of this ultra-Darwinian attitude today—ultra-functionalist attitude today—is the British biologist and popular science writer Richard Dawkins. He asks what job we expect an evolutionary theory to perform.

> The answer may be different for different people. Some biologists, for instance, get excited about 'the species problem,' while I have never mustered much enthusiasm for it as a 'mystery of mysteries.' For some, the main thing that any theory of evolution has to explain is the diversity of life-cladogenesis [branching like a tree]. Others may require of their theory an explanation of the observed changes in the molecular constitution of the genome. I would not presume to try to convert any of these people to my point of view. All I can do is to make my point of view clear, so that the rest of my argument is clear. (Dawkins 1983, 404)

Dawkins goes on to agree with John Maynard Smith (1968) that 'The main task of any theory of evolution is to explain adaptive complexity, i.e. to explain the same set of facts which Paley used as evidence of a Creator.' Jokingly he refers to himself as a 'neo-Paleyist,' concurring with the natural theologian 'that adaptive

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complexity demands a very special kind of explanation: either a Designer as Paley taught, or something such as natural selection that does the job of a designer. Indeed, adaptive complexity is probably the best diagnostic of the presence of life itself' (Dawkins 1983, 404).

But now we have this position challenged. The mantra seems to be 'constraint.' Because of constraints, supposedly natural selection cannot do its job and function is not realized. John Maynard Smith (writing with a group of co-authors) tells us what is at issue: 'Organisms are capable of an enormous range of adaptive responses to environmental challenge. One factor influencing the pathway actually taken is the relative ease of achieving the available alternatives. By biasing the likelihood of entering onto one pathway rather than another, a developmental constraint can affect the evolutionary outcome even when it does not strictly preclude an alternative outcome' (Maynard Smith *et al*. 1985, 269). And, we are told, the study of evolutionary development, reveals many constraints. Hence we cannot rely on natural selection, function is to be downgraded, and other more formal factors are to come to the fore.

Genetic constraints

What about some examples of constraints in action? One much-cited set of examples focuses on so-called 'genetic constraints.' The developmental morphologist Rudolf Raff (1996) invites us to look at the issue of genome size. 'Having a large genome has consequences outside of the properties of the genome per se. Larger genomes result in larger cells. Because cells containing large genomes replicate their DNA more slowly that cells with a lower DNA content, large genomes might constrain organismal growth rates. Cell size will also determine the cell surface-to-volume ratio, which can affect metabolic rates' (p. 304). Salamanders are one kind of organism that often have large genome sizes. Hence, they seem to be good organisms on which to test hypotheses about constraints, and it seems that the formalists do have a point. 'Roth and co-workers have observed that in both frogs and salamanders, larger genome size results in larger cells. In turn, larger cells result in a simplification of brain morphology. Thus, quite independently of the demands of function, internal features such as genome size can affect the morphology and organization of complex animals. Plethodontid salamanders share the basis vertebrate nervous system and brain, but they have very little space in their small skulls and spinal chords' (p. 305, referring to Roth *et al* (1994)).

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The problem is, however, that none of this really excludes a functionalist type of explanation. Raff has to admit that if there are constraints at work, they apparently do not make much difference. The salamanders can do some pretty remarkable things—remarkable salamander things, that is—seeming not at all to be functionally constrained. 'These salamanders occupy a variety of caverniculous, aquatic, terrestrial, and arboreal habitats. They possess a full range of sense organs, and most remarkably, a spectacular insect-catching mechanism consisting of a projectile tongue that can reach out in ten milliseconds to half the animal's trunk length (snout to vent is the way herpetologists express it).'

They have pretty good depth perception too. And indeed, their slow metabolic rate brought on by large genome size may even be of adaptive advantage. 'Plethodontids are sluggish, and the low metabolic rates introduced by large cell volume may be advantageous to sit-patiently-and-wait hunters that can afford long fasts. Vision at a distance is reduced to two handbreadths, but since these animals are ambush hunters that strike at short range, that probably doesn't affect their efficiency much' (p. 306). All in all, there is not much for an ardent selectionist to worry about here, and apparently, if need be, the salamanders can start to bring down their genome sizes. The constraints are just not that strong.

Developmental constraints

This kind of pattern—constraints; need to take seriously formal issues; but not excluding functionalist interpretations—plays itself out over and over again. Consider developmental constraints, and to do this, take the stunning new discoveries in science mentioned at the beginning of this essay. As Darwin pointed out, especially in his little book on orchids, organisms often do not start from scratch. They use what they have at hand and adapt from there. They recycle, in other words. Apparently, at the molecular level, organisms are even greater recyclers of already-available material than they are at the physical level (Carroll 1995; Carroll, Grenier, and Weatherbee 2001). Most remarkable of all are certain so-called 'homeotic genes.' These are not structural genes, that is genes that are coded to make the actual bodily products, but developmental genes that are coded to process the production of bodily products by structural genes. The homeotic genes are those that regulate the identity and order of the parts of the body—a mutation in one perhaps moving an eye to where a leg might normally appear, or vice versa. A subclass of such homeotic genes contains '*Hox* genes,'

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a group of genes to be found in bilaterans (organisms the same on both sides), that order the appearance of various bodily parts, and that seem to work in the sequence as they are found on the chromosomes. In *Drosophila*, the *Hox* genes start up at the head, work down through the thorax, and so on to the end of the abdomen. Within these genes, one finds lengths of DNA, of 180 base pairs, that are used to bind the genes to other DNA segments that are part of structural genes. In other words, these 'homeoboxes' make a protein (of sixty amino acids)—the 'homeodomain'—that is the key to the *Hox* genes actually functioning in regulating the structural genes.

What was absolutely staggering was the discovery of a homology between the homeodomains of *Drosophila* (fruitflies) and other bilaterans, from frogs through fish and mice to humans. Although it has been hundreds of millions of years since humans and fruitflies shared a common ancestor, it is still the case that we use essentially the same chemical mechanisms to order the production of our various bodily parts. The flies' legs and the humans' legs go back to the same processes. The identities are just too great to be chance or even convergence on a common solution. They are homologous. A consequence that leaves some entirely to downplay the significance of selection. The late Stephen Jay Gould (2002), for one, took all of this to be a clear case of the need for a new perspective. Instead of selection, one has certain basic ground plans or archetypes—*Baupläne*—and it is these that really count in evolution, constraining its course and nature. Organisms get certain basic patterns in place, and from then on they cannot escape or do anything outside the constraints set by these unmovable patterns.

Functionalists strike back

But is this well taken? Could it not simply be a case of: 'if it ain't broke, don't fix it'? In other words, could it not be the case that the way that these genes work is adaptive, and that they are kept in place by selection? It works for fruitflies, it works for humans. End of story. Talk of selection not operating because of 'phylogenetic inertia,' or some such thing, is simply unwarranted. For all that Rudolf Raff was one of those quoted above about the triumph of the developmental way, it is he who points out that the genetic homologies may in fact not be all that rigid—suggesting that if selection wants to move things functionally, it can. It is not simply a case of being locked in and unable to do anything else.

Raff discusses a certain *Hox* gene (the Antennapedia complex) that occurs in two species of *Drosophila*, *D melanogaster* and *D*

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pseudoobscura, species that (measured by molecular clocks) parted about 46 million years ago, not that long in the history of life. 'As expected, the clusters of two *Drosophila* species are highly similar in gene composition, arrangement, and conservation of the very long transcription units characteristic of the *D. melanogaster* Antennapedia complex. However, some revealing differences were found. The *Deformed* locus of *D. pseudoobscura* is inverted with respect to the *Deformed* gene in the *D. melanogaster* cluster. The *D. pseudoobscura* orientation of this gene is the primitive one shared with mammals (all Hox genes transcribed in the same order). It was inverted sometime during the 46 million years that separates the *D. melanogaster* lineage from its congeners' (Raff 1996, 309). There are other differences of a like kind, adding up to the conclusion that 'the Hox complex can tolerate substantial change over moderate periods of evolutionary time and within a common body plan.'

In short, no one will deny that homologies—including molecular homologies—exist and are obviously important. A clear sign of evolution and a significant aspect of organic form. But do they—or any like instances of 'phylogenetic inertia'—constrain evolution in any significant way? By analogy, could it not be that 'the fact that all tyres are round more likely means that round wheels are optimally functional than that tyre companies are somehow constrained by the round shape of their existing molds. Thus phylogenetic inertia is not an alternative to natural selection as a mechanism of persistence, and evidence of the former is not evidence against the latter' (Reeve and Sherman 1993, 18)? One needs evidence of more than homology to argue against adaptation. One needs evidence that homology is preventing adaptation.

To be frank, Darwinians suspect that there is something of a slight of hand at work here. The new formalists, people like Stephen Jay Gould, focus on things like the four-limbedness of vertebrates—things that have no obvious adaptive function today. But rather than at once plunging back into a quest for adaptation in the past, when such features first appeared, the formalist focus remains on the present and—thanks to somewhat idiosyncratic (and self-serving) definitions of adaptation, that refuse to apply the term to subsequent uses after the initial use—all that occurs is the labeling of four-limbedness today as 'non-adaptive.' And from there it is all-too-easy to slip into calling it 'non-adaptive' period. A final move is to think up some fancy name like 'archetype' or '*Bauplan*,' giving ontological status to what you are promoting, and the dish is complete. Function is relegated to the sidelines.

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Structural constraints

There are other kinds of putative constraint, including structural constraints—the prime examples of which (in the human world) are the structural constraints of the pillars in mediaeval churches leading (at the points where pillar meets roof) to areas of no function, the much-discussed (in the opinion of some, the overly much-discussed) 'spandrels' of which Gould made so much. Although such spandrels seem adaptive—areas for creative outpourings—in fact they are just by products of the builders' methods of keeping the roof in place. 'The design is so elaborate, harmonious, and purposeful that we are tempted to view it as the starting point of any analysis, as the cause in some sense of the surrounding architecture.' This, however, is to put the cart before the horse. 'The system begins with an architectural constraint: the necessary four spandrels and their tapering triangular form. They provide a space in which the mosaicist worked; they set the quadripartite symmetry of the dome above' (Gould and Lewontin 1979, 148). Perhaps, argues Gould, we have a similar situation in the living world. Much that we think adaptive is merely a spandrel, and such things as constraints on development prevent anything like an optimally designed world. Perhaps things are much more random and haphazard—non-functional—than the Darwinian thinks possible.

To which the functionalist replies: Who ever thought otherwise? No one since Darwin has ever claimed that everything works just right. It is more the case that one should look first for function, and recognize that sometimes it is more complex than simply one thing or another. After all, things like allometry (where body parts are a logarithmic function of the overall body and hence these parts can grow at a much greater rate than the whole) have long been known and acknowledged, and they are the prime example of trying to put a functioning organism together properly and of having trouble optimizing every last feature. The adult, male Irish Elk had a huge set of antlers that may well have been non-adaptive—but this could have come from extreme sexual selection among young males (the Elks were cervine deer, a group where the successful male uniquely keeps and impregnates a whole harem), with much pressure to produce antlers when young, even though when fully adult the antlers proved counter-productive. This would be a case where function worked but then back-fired into non-functionality.

It has also always been agreed that redundant or unwanted characteristics, produced as part of the process of putting things

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together, might later be picked up by selection and used in their own right—as of course are the spandrels of San Marco. Pumping testosterone through the bodies of male humans has all sorts of adaptive virtues—penises and testicles for a start. Perhaps it is indeed the case that a secondary effect is hair on the male face, but despite the best advertizing efforts of the Gillette razor company, it is not obvious that beards are without their adaptative advantages. Or to use Gould's (2002) own favourite example, that the much enlarged clitoris of the female hyena has no present adaptive virtues. It may be that such a pseudo penis came by chance, but this does not deny its value today in mating rituals.

In fact, it has always been a key part of Darwinism that side effects can be a crucial part of the evolutionary story. A big question is about how new characteristics ever get started. As Gould forever asks, could a tenth of an eye be of any great value? Well, as Dawkins (1986) responds, perhaps it could, but there is no need to suppose immediate value in every new feature. Feathers today obviously have the adaptive edge when it comes to flying, and no one would say that flight is without its purposes. Increasingly, however, the evidence is that feathers first appeared on the dinosaurs, not for flight, but for other ends, most likely insulation and heat control. Only later were they used to invade the air.

Physical constraints

There are other potential types of constraint. Particularly interesting are physical constraints. Why do we never get a cat as big as an elephant? Because size and consequent weight goes up rapidly, according to the cube power of length or height. Suppose you have two identically shaped mammals, one twice the height of the other. It is going to be eight times as heavy. This means that from, a structural perspective, it has got eight times the weight problem. You simply cannot build elephants as agile as cats. They need far more support, which in turn means bigger and more stocky bones (Vogel 1988).

Another interesting calculation concerns what has irreverently been called the 'Jesus number.' What are the constraints on walking on water? In fact, a fairly simple formula governs the activity. Pushing up is the surface tension, γ, times the perimeter of the feet or area that is touching, l. Pushing down is gravity, which is a function of the mass, m, times the gravitational attraction, g ($F = mg$), or restating in terms of density, ρ, times the volume, which is a function of l cubed. In other words: $Je = \gamma l/\rho l^3 g = \gamma/\rho l^2 g$. Since the surface tension, the density, and the gravitational constant remain

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the same, this means that the ability to walk on water is essentially a function of the perimeter squared. In other words, the smaller you are the better off you are, and conversely the bigger you are the more likely you are to sink. This is no problem for insects, especially given that they have six legs and so have a lot of perimeter for the body size. Humans however are another matter. 'What would be the maximum weight of a human who could walk on water? My size-9 sandals have a perimeter of 0·62 meters each; that length times the surface tension of water gives 0·045 newtons of force, or 4·6 grams (less than half an ounce) of weight—9·2 grams to stand (two feet in contact) or half that to walk. The theological implications are beyond the scope of the present book' (Vogel 1988, 100). This essay too!

However the philosophical implications are clear. There is more to life than simple function, but even in a case like this the functionalist will see selection at work. The point is that organisms exploit physical constraints for their own ends. John Maynard Smith and his co-authors have explored in depth the example of the coiling of shells in such organisms as molluscs and brachiopods. The coiling itself is fairly readily reduced to a simple logarithmic equation and it is possible to draw a plain that maps the coiling as a function of the vital causal factors, particularly the rate of coiling and the size of the generating curve. Given such a map, one feature stands right out for comment: whereas for most shells the coils touch all the way from the centre to the perimeter, some such shells coil without touching. There is a gap between the coils. Now, map the actual shells of a group of organisms, for instance, the genera of extinct ammonoids (cephalopod molluscs), including the theoretical line dividing touching coils from non-touching coils. The isomorphism between the theoretical and the actual is outstanding.

> [N]early all ammonoids fall on the left side of the [theoretical] curved line and thus display overlap between successive whorls. This is clearly a constraint in the evolution of the group but what kind of constraint? In this particular case, the answer is apparently straightforward... Evolving lineages can and occasionally do cross the line so there is no reason to believe that open coiling violates any strict genetic or developmental constraint. Rather, the reason for not crossing the line appear to be biomechanical. Other things being equal, an open coiled shell is much weaker than its involute counterpart. Also, open coiling requires more shell material because the animal cannot use the outer surface of the previous whorl as the inner surface of the new whorl. (Maynard Smith *et al.* 1985, 280)

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Even the exceptions prove the point. The shell of the living pelagic cephalopod Spirula has a shell that coils but does not touch. Exceptionally, this organism carries the shell internally, using it for buoyancy. There is no need for strength.

Maynard Smith and co-authors conclude 'that the constraint against open coiling is an adaptive one brought about by simple directional selection.' A conclusion which surely brings us full circle, for if constraints can be *adaptive*, brought on by selection, the distinction between form and function has truly collapsed. Indeed, theoretical biologist Gunter Wagner (1988) goes so far as to argue that constraints may be necessary for the action of selection, else variation will be all over the place with any positive changes being outweighed by other moves in a wrong direction.

Conclusion

Enough has been said. Around about 1959, the centenary of the publication of the *Origin*, functionalism was just about the only game in town. Apart from a few despised German morphologists and one or two idiosyncratic philosophers, no one had any time for a formalist approach to nature. Now things have swung the other way, and in some evolutionary circles, formalism rules triumphant. However, pulling back and looking at biology as an outsider—as a philosopher that is—one can see that things are not quite this simple. As the above discussion shows, a case can be made for formalism. But equally, as the above discussion shows, a case can still be made for functionalism.

In this sense, one should probably not speak of rival paradigms, but rather of different elements that go to make up the overall complete picture. But one senses that, historically and philosophically, there is more to be said than this. Historically, the form-function dichotomy—form-function tension rather—goes back to Aristotle and forward to today, right across the coming of evolution. And philosophically one does see some of the features of a paradigm, inasmuch as—rather like the Gilbert and Sullivan operetta, where every little child that is born into this world alive, is either a little Liberal or a little Conservative—biologists do seem to split over whether one should think form first and function second (and reluctantly at that), or function first and form second (and reluctantly at that).

Darwin, to take one example, was an out-and-out functionalist. He recognized form—he spoke of homology as Unity of Type—but saw it as coming from function. Gould, to take the other extreme,

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was an out-and-out formalist, and he saw function as coming a distant second. His hero was the early twentieth century Scottish morphologist, D'Arcy Thompson, who had no sympathy with the Darwinian's focus on final cause, and who argued strenuously that material and formal causes are prior and more important. 'To seek not for ends but for antecedents is the way of the physicist, who finds "causes" in what he has learned to recognise as fundamental properties, or inseparable concomitants, or unchanging laws, of matter and of energy. In Aristotle's parable, the house is there that men may live in it; but it is also there because the builders have laid one stone upon another' (Thompson 1948, 6). Continuing: 'Cell and tissue, shell and bone, leaf and flower, are so many portions of matter, and it is in obedience to the laws of physics that their particles have been moved, moulded and conformed. ... Their problems of form are in the first instance mathematical problems, their problems of growth are essentially physical problems, and the morphologist is, *ipso facto*, a student of physical science' (p. 10). Thus: 'We want to see how, in some cases at least, the forms of living things, and of the parts of living things, can be explained by physical considerations, and to realise that in general no organic forms exist save such as are in conformity with physical and mathematical laws' (p. 15).

We have different perspectives, different visions. In this sense, we do have different paradigms. And, let me stress, in case you think I am ambiguous or disapproving, this is no bad thing. I do not see this as a sign of weakness in biology or of immaturity. If a division has been around for 2500 years, and is thriving today as never before, I doubt it is going to go away in a hurry. But the point I would make is that because biologists are motivated to go out and make their case—form or function—some terrific science gets done. The divison is incredibly creative. So let us not regret it, but rejoice in it. The task now for philosophers is to try to understand it. What is this modified notion of 'paradigm' with which I am playing? Is it unique to biology or can it be found elsewhere in science? And what does this tell us about such issues as objectivity and subjectivity? These are the questions to which we philosophers should turn now.[2]

[2] I do not pretend that I am the first to discover the kind of entity that I am calling a 'paradigm.' In a way, it seems to me to be much like what Karl Popper (1974) called a 'metaphysical research programme.' I am not, of course, claiming that Popper would agree that form and function are exemplars of such a notion. One thing that does seem important to this notion as I am using it is the idea of metaphor. We are seeing the world as if it were an object of design—utilitarian or formal. I explore this kind of

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thought in my *Mystery of Mysteries: Is Evolution a Social Construction?* I note with some interest that Kuhn (1993) himself tied in paradigm thinking with metaphor.

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