

Can the New Science of Evo-Devo Explain the Form of Organisms?

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The answer is: No — form is needed to do the explaining.

1 Introduction

What is so frightening about the form of living things? Nothing, it might seem. Much of our biological science is a science of form, a science whose task is to understand why proteins and cells, tissues and organs, plants and animals have the form they do, and how they get that way.

But what is so frightening about the form of living things? Everything, it might seem. For the treatment of form in biology is continually “hushed up” in explanations that are as devoid of form, as silent about form, as we can possibly make them.

Today in particular we find powerful urges to engage the problem of organic form with scientific understanding, and yet an equally powerful reticence to reckon with or even acknowledge the forms we can so readily see, as if every such form somehow masked a shameful or threatening countenance.

The problem of form has long been central in the life sciences, where each creature so notably reproduces after its own kind — according to its own form. “It is hardly too much to say,” wrote geneticist C.H. Waddington, “that the whole science of biology has its origin in the study of form.” The description of plants and animals, the identification of separate and discrete organs, the comparison of related types in evolutionary theory — through activities like these, Waddington notes, biologists “have been immersed in a lore of form and spatial configuration” (1968, p. 43).

And yet that great student of animal form, Adolf Portmann, could already write in 1952 that the pursuit of invisible causes was alienating biologists from the living appearances available to their senses. “More and more laboratory work is becoming restricted to the skillful selection of just a few animal species, those which might be called the domestic animals of science. What opportunity is left for observing that countless number of different living forms which is part of the earth’s riches?” (1967, pp. 17–18).

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Today, moreover, we can hardly say that attention is focused in any full sense on even a few animal species. Rather, our impressive technical skill is brought intensively to bear on this or that tissue and, ultimately, on a set of molecules extracted from those tissues. The organisms themselves — those wonders of endlessly diverse and endlessly expressive form — have become more or less incidental to the laboratory technician.

2 The Unreasonable Effectiveness of Natural Selection

If the researcher tends to avert his gaze from the form of the living, functioning organism, we can reasonably wonder why. And we may be reminded of the famous case where Charles Darwin recoiled from his contemplation of the subtle perfections in the form of the eye: “To suppose that the eye, with all its inimitable contrivances for adjusting the focus to different distances, for admitting different amounts of light, and for the correction of spherical and chromatic aberration, could have been formed by natural selection, seems, I freely confess, absurd in the highest possible degree” (*Origin of Species*, Chapter 6).

Of course, as Darwin quickly added, his theory convinced him that he was merely suffering from a lack of imagination. All that was really needed were the creative powers of natural selection acting through eons upon an endless supply of small, helpful changes. But his underlying malaise was not so easily vanquished: “It is curious,” he wrote to the American botanist Asa Gray in the year following publication of the *Origin*, “that I remember well [the] time when the thought of the eye made me cold all over, but I have got over this stage of the complaint, and now small trifling particulars of structure often make me very uncomfortable. The sight of a feather in a peacock’s tail, whenever I gaze at it, makes me sick!” (Darwin 1860).

We can assume that Darwin got over that stage of the complaint as well. But, thankfully, the biologist is still now and then allowed, if not a complaint, at least an honest expression of wonder. Portmann, writing not of the peacock, but of another bird with a remarkable pattern of coloration on its wings, asked us to appreciate the difficulty of explanation:

If... we look at the speculum on a duck’s wing, we might imagine that an artist had drawn his brush across some ten blank feathers, which overlap sideways — making white, bluey-green, and black lines — so that the stroke of the brush touched only the exposed part of each feather. The pattern is a single whole, superimposed on the individual feathers, so that the design on each, seen by itself, no longer appears symmetrical. We realize the astonishing nature of such a combined pattern only when we consider that it develops inside several or many feather sheaths completely separated from one another; and that in each individual feather it appears at an early stage while it is still tightly rolled up, the join pattern not being produced until these feathers are unfolded. What sort of unknown forces direct the construction work in the ‘painting’ of these feather germs? (Portmann 1967, p. 22).

Natural selection, it appears, works to perfection in the creation of form. But how are we to understand this perfection? What sort of explanation are we looking for when we want to make *sense* of form? In the case of that patch of color on the duck’s wings: will it be enough when we have traced the processes and connections by which the molecules of pigment come to be present in the various feathers? Do we need to discover

also some *use* for the design? And what about the form itself — its expressive character and beauty? Do these have no place in science?

Quite apart from the peacock and duck, there are, Portmann points out, countless cases where animals produce striking visual patterns that either are not seen at all or are of no as yet conceivable relevance to survival. As historical psychologist Jan Hendrik van den Berg puts it,

Whoever talks about perfection (usefulness, efficiency) utters an *understatement*. Animate nature possesses *lustre*. Each animal, each plant, radiates splendor and glory. Animate nature isn't only a business that is working well; it is a garden of luxury and abundance. Does anyone need examples? The sheen on the feathers of a sparrow — unnecessary. The droplet in the middle of the leaf of the common lady's mantle. The swan on the water. . . peacock butterflies, young foxes. Hogweed in full bloom with the dozens of diptera. The white umbellifer of the wild carrot, with its one red flower in the middle. (1984, p. 73; emphasis in original)

“Lustre” does not sound very much like a scientific category. But where *do* we find scientific categories amid all this luxuriance and perfection of form?

3 Controlling Genes . . .

Biologists have long confronted two distinct challenges to explanation: How does form arise in the development of an individual organism, and how is this form achieved over the course of evolution? Over the last couple of decades these challenges have been addressed and to some degree united through a flourishing collaboration between two disciplines: developmental biology and evolutionary developmental biology. Sean Carroll, a geneticist and prominent researcher in the new field, tells its story in his book, *Endless Forms Most Beautiful: The New Science of Evo Devo* (2005). To Portmann's question, “What unknown forces direct the painting of the duck's speculum?” Carroll and many of his colleagues are convinced they have the answer, at least in principle.

A researcher at the Howard Hughes Institute and a professor of genetics at the University of Wisconsin in Madison, Carroll begins his book by quoting physicist Jean Perrin to the effect that scientific advance requires us “to explain the complex visible by some simple invisible.” In Carroll's case, this principle leads to a preoccupation with “the invisible genes and some simple rules that shape animal form and evolution.” What is remarkable in his telling of the story is that many of the very *same* genes control the making of both an insect's body and our own, something that “not a single biologist. . . ever anticipated” (pp. ix–x). The claim issuing from this discovery is that the enormous diversity of living creatures results mostly from recombinations of the same ingredients.

Carroll's triumphalist narrative focuses heavily on the role of “tool kit” or “master” genes. Until their discovery, biologists had known that “evolution is due to changes in genes, but this was a principle without an example. No gene that affected the form and evolution of any animal had been characterized” (p. 8). That state of affairs ended with the identification of a relatively small number of genes whose presence, absence, or mutation is associated with the formation (or deformation) of large-scale, discrete features of an organism — and often associated with similar features in widely differing

organisms. These tool kit genes may, for example, produce proteins that are distributed in bands, stripes, lines, or spots throughout a young embryo. This geographical distribution turns out to be a kind of map of the features that will develop later.

Carroll reproduces beautiful photographs of fly embryos showing (by means of technical manipulation) brightly colored regions, where each region — blue, green, red, yellow — corresponds to the activity of a particular collection of genes. A couple of hours after fertilization, the oblong embryo is about one hundred cells in length from end to end (or from “west” to “east,” as the researchers prefer to say, with west corresponding to the future head pole). Thanks to the activity of tool kit genes, the western, middle, and eastern sections of the embryo clearly reveal themselves as separate bands. As these bands fade, they are replaced by seven stripes over the eastern two-thirds of the embryo. Each stripe, together with the neighboring darker band, marks out a pair of future segments of the fly larva. Then these stripes, too, under the influence of yet another group of genes, give way to fourteen stripes indicating the fourteen segments of the larva individually. Most of these latter stripes persist throughout development, and they lead rapidly to actual segmentation of the embryo.

The photographs are spectacular, and leave no doubt in one’s mind that the early embryo, uniform and undistinguished as it might appear under ordinary light, is in fact an embodiment of order and form. There is a head and tail, with degrees of longitude between them, and likewise a top and bottom (dorsal and ventral), with degrees of latitude. And different regions (Carroll calls them “modules”) are already marked out for the development of specific organs and appendages.

Carroll’s own work has focused on butterflies. Here again the design to come is signaled by the distribution of tool kit proteins. And here, too, Carroll produces photographs showing these proteins in the developing wing, occupying exactly those locations where the beautifully decorative spots and stripes and rings will eventually appear. It’s as if the future design were in some way already there.

4 . . . And Master Switches

But tool kit genes are only part of the picture. It’s true that the protein bands in the early embryo are associated with tool kit genes that are activated in those bands so as to produce (“express”) the proteins. Certain genes that are “on” or “off” within the band, will be in the opposite state outside the band. But what is supposed to coordinate this activation and deactivation of genes? Carroll’s answer is at the same time his central theme: the tool kit genes are systematically turned on and off by an “operating system” — a vast network of switches residing in the non-coding portions of DNA. Like a global positioning system (GPS), these switches “integrate positional information in the embryo with respect to longitude, latitude, altitude, and depth, and then dictate the places where genes are turned on and off.”

Each switch is actually a short stretch of DNA associated with a particular tool kit gene. Often there are multiple switches for a single gene. Proteins (produced by yet other tool kit genes) can bind to these switches, altering their state, and the overall pattern of switch states for a particular gene determines whether that gene will be activated or

repressed. This allows a single gene to be used in many different ways at different times and places — for example, in the development of the heart, eyes, and fingers. Everything depends on the states of its associated switches. “The entire show,” writes Carroll, “involves tens of thousands of switches being thrown in sequence and in parallel” (p. 114).

The computational powers of this controlling network of switches, Carroll tells us, allow fine-grained management of the expression of individual genes. But at the same time the switches are the key to modularization of the organism, making it possible for entire features (a spot on a wing, an insect’s eye, a digit on a mammal’s foot) to come or go — or be modified in dramatic ways — with the flip of a few switches. This, he suggests, has implications not only for the development of the individual organism, but also for the evolution of species.

There is, after all, a remarkable degree of commonality in the gene sets of organisms far removed from each other in evolutionary time. It’s not just that the DNA of humans and chimpanzees is about 98.8 percent identical; “96 percent of all genes in the human are found in the exact same relative order in human chromosomes as in the mouse chromosomes” (pp. 268–70). If genes, with their fewer-than-expected changes over the course of evolutionary history, are not by themselves adequate to account for the differences between species, then what does account for those differences? The controlling network of switches in non-coding DNA. Carroll is convinced that changes in these switching networks have done a lot of the work of evolution — more than can be achieved through the mutation of genes themselves

5 The Many Guises of Form

All this raises an obvious question, which Carroll himself acknowledges. Suppose we have a fly embryo divided into three regions marked out by proteins A, B, and C.

You might ask, where do these patterns of tool kit proteins A, B, and C come from? Good question. These patterns are themselves controlled by switches in [the associated] genes A, B, and C, respectively, that integrate inputs from other tool kit proteins acting a bit earlier in the embryo. And where do those inputs come from? Still earlier-acting inputs. I know this is beginning to sound like the old chicken-and-the-egg riddle. Ultimately, the beginning of spatial information in the embryo often traces back to asymmetrically distributed molecules deposited in the egg during its production in the ovary that initiate the formation of the two main axes of the embryo. . . I’m not going to trace these steps — the important point to know is that the throwing of every switch is set up by preceding events, and that a switch, by turning on its gene in a new pattern, in turn sets up the next set of patterns and events in development. (p. 116)

Here, then, is the general thrust of Carroll’s attempt to “explain the complex visible by some simple invisible” and to elaborate “the simple rules that shape animal form.” But perhaps we may be forgiven a certain unease at this point — a discomfort owing not so much to the series of ever-receding inputs that peter out in a vague appeal to “asymmetrically distributed molecules,” and not so much to the questionable simplicity of “tens of thousands of switches being thrown in sequence and in parallel,” as to a cer-

tain nagging doubt. It's a doubt about the way Carroll conceives his entire project. He claims to be *explaining* form. In what sense does the work in evo-devo explain the form of a developing organism?

Carroll, with his beautiful photographs, does a wonderful job of tracing the manifestation of form in certain of its aspects. With his help we can recognize the form in a more dynamic sense than when we imagine it as something finally frozen in the "finished" organism. Every living form is a form of movement. But in tracing the manifestations and metamorphoses of form are we doing anything more than just that? In particular: are we elucidating a set of intrinsically formless mechanisms that bring the organism's form into existence from a preceding formlessness? Are we outlining simple, formless rules that determine and shape a great complexity? So far as the evidence Carroll adduces is concerned, what we are witnessing is not the explanation of form by something else; rather, what he gives us is an elaborated picture of the unfolding of form. And that is a very great deal — much more, in fact, than he seems to want to credit himself with.

If we are trying to explain form as the result of something other than form — as the result of supposedly formless mechanisms and simple rules — then to say that a pattern of tool kit gene expression prefigures the future pattern of segments, organs, appendages, or color designs doesn't do the job. We are still explaining pattern by pattern, and therefore are only relocating the form we need to explain. How did the prefiguring pattern arise? And if a still earlier complex pattern of gene expression prefigures that one, how did the earlier pattern arise? And if the entire sequence is rooted in asymmetries of molecular distribution in an egg cell — that is, in the internal *form* of the cell — well, it seems we never do get the kind of mechanical explanation of form we were looking for. Maybe we were looking for the wrong sort of explanation.

Nothing much changes when we consider the almost unfathomably intricate pattern of the DNA network "programming" to which Carroll appeals. While switches are one thing, perhaps comforting in their mechanical familiarity, the pattern informing the entire network of switches — the almost inconceivably intricate pattern corresponding to and shaping the eventual manifest form of the organism — is quite another. The governing image or idea at work in this organized throwing of switches — the idea that will eventually manifest itself in the visible form of the organism — may be subtle and difficult to trace, but this only makes its reality as pattern and its effective governance all the more impressive.

Our own experience in creating such program logic is unambiguous. You and I could write a computer program to produce the form, say, of Da Vinci's "Last Supper," but in doing so we would be *starting* with the form of the painting, imposing it upon the computer's logic with concerted, form-conscious effort. Do we ever see a production of form in a living organism where the developing form does not already *inform* the manifestation at every stage? Can we even conceive what it might mean to explain the arising of form through an appeal to something inherently formless? And if not, can we safely take it for granted that the artistic language we use for the elucidation of form — the language developed by those who have worked most intimately with form — is irrelevant to the neglected science of form?

Of course, despite all our direct experience with the production of form, we are well accustomed to thinking that nature somehow achieves its sculptural feats without prior reference to form, which is supposed to be a result rather than a cause. But the question is whether this is anything more than a habit of thought — and an unhealthy one at that. Our sustained inattention to form in its own terms over these past few centuries makes it all too easy for a scientist like Carroll to rely heavily upon an unrecognized appeal to form even while thinking himself to be explaining form as the mere result of simple mechanisms and rules.

6 Glimpses of Nature as an Artist

In facing the problem of form, Carroll seems to feel at least a nascent, half-conscious urge to consider form in its own terms, rather than immediately reconceive it as a computational problem of switches and other genetic devices. *Something* lures him toward the language of form — which is to say toward the language of art — as when he repeatedly speaks of the organism being *sculpted*. The *ubx* gene, he says, “sculpts the form of [the fly’s] hindwing.” Likewise, serially repeated structures such as vertebrae and ribs “are sculpted by Hox proteins.” And “the general logic of tool kit genes’ action in organizing, subdividing, and specifying and sculpting parts of the embryo becomes clear when visualized” (2005, pp. 91, 127).

For all the emphasis upon genes and switches, this mention of visualization testifies to much more than logic, as Carroll himself seems to acknowledge. Citing “the beautiful patterns of gene expression” displayed in embryos, he remarks of DNA switches: “Part genetic computer, part artist, these fantastic devices translate embryo geography into genetic instructions for making three-dimensional form” (p. 111).

Somehow this reference to the artist seemed appropriate to Carroll, despite the fact that it sits so uncomfortably alongside “computer” and “genetic instructions” — the artist, after all, does not create by following a set of instructions, computational or otherwise. Unfortunately, Carroll never attempts to reconcile his conflicting terminology, and one gets the feeling with him, as with so many other scientists when they write for the general public, that the artistic language remains casual and unconsidered; something about it may “feel right,” but its use is more a matter of rhetorical effect than scientific substance. His *explanations* are all about computational switching networks and not at all about artistic coherence. We can guess that, if pressed, Carroll would say his references to artistry and sculpting were “just metaphors.”

But this would be to ignore the questions at hand. Why do the metaphors work so naturally? Why do they feel right? Could it be that they actually play a subtle and unrecognized supportive role in our interpretation of the research Carroll describes? Do they make it easy for us to import imaginal significance into the action of genetic devices — a significance that those devices themselves cannot support? And is the role of those devices in explaining form therefore illusory?

Whatever the case, it would not be wise to underestimate the force of a compulsion capable of driving biologists toward artistic metaphors despite long-established sanctions against taking such metaphors seriously. Listen to Darwin’s great apologist, Tho-

mas Huxley, describing the same embryonic development Carroll is concerned with:

Examine the recently laid egg of some common animal, such as a salamander or a newt. It is a minute spheroid in which the best microscope will reveal nothing but a structureless sac, enclosing a glairy fluid, holding granules in suspension. But strange possibilities lie dormant in that semi-fluid globule. Let a moderate supply of warmth reach its watery cradle, and the plastic matter undergoes changes so rapid and yet so steady and purposeful in their succession, that one can only compare them to those operated by a skilled modeller upon a formless lump of clay. As with an invisible trowel, the mass is divided and subdivided into smaller and smaller portions, until it is reduced to an aggregation of granules not too large to build withal the finest fabrics of the nascent organism. And, then, it is as if a delicate finger traced out the line to be occupied by the spinal column, and moulded the contour of the body; pinching up the head at one end, the tail at the other, and fashioning flank and limb into due salamandrine proportions, in so artistic a way, that, after watching the process hour by hour, one is almost involuntarily possessed by the notion, that some more subtle aid to vision than an achromatic, would show the hidden artist, with his plan before him, striving with skilful manipulation to perfect his work. (Quoted in Barfield 1963, pp. 144–5)

To raise the question of metaphor here is really to ask how far we can trust the terms of our own seeing. Do we really need some still more subtle instrument that will reveal a hidden artist working from outside — which, of course, Huxley didn't believe in — or do we need rather to credit the capacity of our own, educated eyes to see what *informs* the processes right there in front of us? The embryo plainly and objectively manifests a power of unified expression, of metamorphosing organic form — something a child can recognize. Where we see systematically experienced form in natural phenomena, why should we doubt that the language of form — the essentially noetic, immaterial, aesthetic language of form — naturally evoked by these phenomena, whether under the eye of a child or a Thomas Huxley, is intrinsic to our objective understanding of them?

The scientist's immediate reaction to the recognition of form is to look for explanatory causes, such as Carroll's genetic switching systems, that are presumed to act autonomously, without reference to form. But can't we have the switching systems (if that is indeed the proper term) *within* the context of form, instead of as presumed explanations of that form?

7 The Play's the Thing

Carroll would surely acknowledge that to speak of the *ubx* gene sculpting the form of the fly's hindwing is to appeal to a cause that drastically underdetermines its supposed effects. It takes an entire organism to sculpt a hindwing, something Carroll already suggests with his mention of those thousands of switches being thrown in a coordinated manner. And so, with a view toward this larger picture, he rightly stresses the importance of context. Referring to the fact that "the same gene involved in building fruit fly limbs and arthropod limbs appeared to be doing something altogether new in butterfly wings," he admonishes us: "Remember, everything about a tool kit protein's action depends on context" (p. 208).

But what is context if not form? A random collection of things is not a context — not until a set of unifying relations ties them together in a recognizable and sustainable

pattern. What makes a context a context is this set of relations — *relations that evolve in their own whole and coherent terms*. If the biologist's genes and switches are not form-elements — if they are not caught up within, and given their significance by, a pattern of some sort — then they cannot add to our understanding of the organism's developing form. If, on the other hand, the genes and switches *do* reveal themselves as elements within an organizing pattern or form, then it is this form, in combination with all the other organizing patterns, that constitutes our understanding of the organism and brings the “genes and switches” into this understanding.

The crucial distinction here has long been recognized, but because of a one-sided science education, at least in the United States, it tends to feel difficult and alien to the thinking of many working researchers. I mean the distinction, for example, between the physical analysis of a work of significant form and the characterization of it as a work of significant form. Taking the example of an artistic work: to describe the processes by which paint arrived on the canvas or by which the hammer and chisel removed chunks of marble is to remain a long way from any apprehension of the form we discover in a painting or sculpture.

Portmann uses a theater stage production to make the same point, remarking that “whether we are able to understand the play which is being enacted before our eyes depends upon other requisites than a grasp of the technique of the performance”:

We may watch the way in which the actors get ready, how the machinery produces the effects of thunder and rain; how everything works together so that, by the complicated action of many invisible helpers, a play having an intelligible sequence is finally unfolded before the spectator. But such a glimpse behind the scenes tells us neither the gist of the play nor its significance.

And when we *do* gain understanding of the play, we can hardly pretend that it is *explained* by the stage machinery. Actually, explanation runs more strongly in the other direction. The meaningful form of the stage production is what enables us to make sense of the diverse hustle and bustle of technical activity. The stage devices and all the mechanics of the performance are not so much the causes of the forms observed onstage as they are expressions of it.

Applying the analogy, Portmann grants that “physiologico-genetic research is necessary; but there is also another question to be asked about the meaning of appearance as we see it” (1967, pp. 161–4). But this requires some unpacking.

8 On Form and Explanation

The reason we cannot explain form is that the appeal to form is what explanation *is*. We gain understanding by recognizing significant form. So the attempt to explain form is an attempt to explain explanation; we have to assume what we are trying to explain — which, in fact, is what we saw Carroll doing with his explanation of butterfly forms.

The botanist approaching, say, an oak or a weeping willow from a great distance will at some point see it clearly enough to exclaim, “Oh, *that's* what it is!” This recognition of a particular, unified character expressed in the visible form of the tree is understanding.

We cannot gain such an understanding from the mere aggregation of particulars, but only from our recognition of the way they hold together as an *image*.¹ Everyone possesses this understanding to one degree or another — it's hard not to recognize at least some of the distinctive imaginal character of the weeping willow and oak.

While the field botanist has a much more systematic and refined knowledge of such distinctions than the common person, we can safely assume that his knowledge is far from complete — especially when framed only in terms of the external features of a plant. But that initial moment of recognition from a distance, when the visible features suddenly “come together” in his imagination as a coherent form, illustrates the essence of understanding. It's the kind of *seeing* that always satisfies us as *knowing*, and can do so only because it is imbued with the thought-content that makes a phenomenon *manifest* — with the imaginal concepts that give us an appearance of distinct, recognizable character. Where earlier the vaguely discerned elements made no sense and had no systematic connection with each other, now they all “fit together” by virtue of occupying their proper place within a larger picture.

What remains is to extend this imaginative, pictorial, gestural recognition to all the other, not immediately visible aspects of the oak, from its inner growth rings and cellular structure to its DNA. But at each of these further steps we gain our understanding in much the same way: “Oh, *that's* what it is!” — Oh, *that's* the picture, the pattern, the form that holds these details together. And the possibility of there being any true science depends on our finding that nature does indeed hold together in this way through and through — and therefore that the botanist's initial recognition of the oak based on its overall outward form will be “of a piece” with its various smaller-scale and invisible forms and movements. In this way we can hope to approach ever more fully what might reasonably be termed the *idea* — in other words, a scientific understanding — of the oak.²

This imaginal idea is what once was referred to as the *formal cause* of the oak. It stands in contrast to the usual notion of cause as a precise, isolated, well-defined determinant of a precise, isolated, well-defined effect — which, despite having proven so indigestible to philosophers, remains for most scientists the central feature of explanation. And yet, actual experience shows *governing form* — our discovery of the patterning of things — to be the primary source for our sense that something has been explained. After all, the mere fact of the existence of mechanically effective “genetic switches” could not by itself have convinced Carroll that he was onto something. What rightly excited him was the discovery of a pattern of activity governing those switches — a pattern clearly expressing, at various stages of development, something like the same idea, the same coherence, the same unified principle of organization already noted in the visible

¹ It is a valuable exercise to contrast the immediate recognition achieved by the botanist who thoroughly knows a plant, with the kind of identification process we go through when using a key — that is, a typical field guide that leads one step by step through what are often very minute details. See Talbott (2005).

² For a wonderful exposition of the role of the idea in our seeing and understanding, see chapters 1, 4, and 8 by Ronald Brady in the book, *Being on Earth* (Maier, Brady, and Edelglass 2006). It's available at <http://natureinstitute.org/txt/gm/boe>.

characteristics of the butterfly wings. He was not explaining that form; he was finding further differentiated expressions of it in time — a valuable contribution to our understanding. He was explaining by *means* of form.

The feeling that we ought to explain form is a central distorting element in the practice of science today. It conceals from us the essence of our own activity and achievement as scientific knowers. Goethe recognized two centuries ago that the apprehension of form — living, dynamic, essential form — is what explanation most essentially *is*. It was he, in fact, who pioneered the science of organic form and who gave us the term “morphology,” saying of this new science that “its intention is to portray rather than explain” (1995, p. 57). A portrayal is image-like, and without such an imaginal form nothing holds the particulars together so as to make *sense* of them; they merely coexist meaninglessly. In seeking portrayal rather than explanation, Goethe was not rejecting the notion of explanation in its broader sense as the articulation of understanding, but only in the too-narrowly-focused, non-explanatory sense professed in so much of science today.

9 A Justified Incredulity

Confusion about the nature of scientific explanation accounts for a great deal of the misdirection in contemporary disputes about evolution. One way to get at this misdirection is to recall a private remark by Darwin, who could at times be touchingly honest about his personal doubts and feelings. It happened that during the last year of Darwin’s life the Duke of Argyll mentioned to him “the wonderful contrivances for certain purposes in nature” revealed in Darwin’s own published works, such as his treatises on the fertilization of orchids and on earthworms. As the Duke later described the ensuing exchange, “I said it was impossible to look at these [contrivances] without seeing that they were the effect and the expression of Mind. I shall never forget Mr. Darwin’s answer. He looked at me very hard and said, ‘Well, that often comes over me with overwhelming force; but at other times,’ and he shook his head vaguely, adding, ‘it seems to go away’.” (Francis Darwin 1902, p. 64)

It’s not the sort of personal openness you’re likely to hear today from battle-tested Darwinian apologists and intelligent design advocates! And it leads one to wonder whether the coming and going of Darwin’s conflicting cognitive moods might have reflected a deep-lying misunderstanding about what constitutes explanation. Today, in any case, when the heirs of both Darwin and the Duke of Argyll have hardened their positions, the misunderstanding has come into clear relief. When evolutionary biologists hear someone express wonder over the mammalian eye or peacock’s feathers, and when this wonder shades into incredulity about the usual sort of explanation for such things, all too often the biologists’ immediate assumption is that they’re up against an antagonist who doesn’t believe the eye or feather can be understood scientifically and who therefore wants to invoke some extra-scientific, and perhaps miraculous, explanation. And in fact some of the critics of evolution want to do exactly this.

More promisingly, we can step out of that fractious dispute and view the battlefield from a new level, where it becomes possible to grant the legitimate concerns of both sides. The scientist is absolutely justified in demanding unexceptioned respect for law-

ful, normal physical and biological process. Any attempt to introduce violations of this process leads immediately to nonsense.

But at the same time the incredulity the critic feels when contemplating the wonders of biological form is fully and emphatically justified. We *should* look at the eye and feather with disbelief in the usual manner of explanation. This, however, is not because we need miracles or violations of physical law. No, what we are disconcerted about is the claim that form has been *explained* by a description of processes from which considerations of form have been excluded as far as possible. Our unease is with the incommensurability between the explanation and what it is supposed to explain. The incommensurability, as I've tried to show above, results from the attempt to explain form by reference to mechanisms assumed to be both independent of form and the causes of it — when in fact we can make sense of the so-called “mechanisms” only by reference to the form we are supposedly explaining. Starting with the most minute physical beginnings of the organism, the scientist is always looking for the organizing, forming, informing, meaningful ideas that give shape and coherence to the unfolding drama. If the undeniable presence of those “mentalist,” informing ideas points us beyond narrow, physicalist conceptions of the world — well, we have no choice but to let the world speak for itself. But we should not distort this speaking by interpreting it as a miraculous violation of the physical order — no more than we interpret the immaterial meaning of human speech as a violation of the physical principles of air movement.

It's true that when Portmann described the remarkable features of the duck's speculum, he wondered out loud how the processes involved could possibly be understood. But, given who Portmann was, we can be absolutely sure that he believed there was a perfectly legitimate scientific understanding to be had, if only we could find it. After all, the speculum is *there* as a physical reality, so we know there is some means of physical realization. The pattern gets there step by step, and if we were able to accompany this development with the correct insight, we would surely see the speculum coming into existence without any breaks, miraculous or otherwise, in the physical processes. It all happens right before our eyes. If it seems impossible to us, perhaps this is because we have for so long toyed with insufficient, wooden concepts of cause and effect and therefore have ceased to notice how form, with endless imaginative verve and endlessly surprising resourcefulness, clothes itself in physical substance.

All this gives us a proper perspective upon Carroll's response to the claim that “the living cell is an entity of irreducible complexity.” The claim is empty, he says. Those who make it have been “counting on biology to hit a wall in reducing complex phenomena to molecular processes,” but their “pessimistic forecasts have been obliterated in the continuing revolution in the life sciences” (Carroll 2005, p. 298).

Yes, in Carroll's sense we can always “reduce complex phenomena to molecular processes.” That is, we can narrow our gaze, removing from sight the relevant contextual and shaping ideas that, nevertheless, remain as a kind of vague, ideational haze around our mechanistic picture of those molecular processes. But this is only to conceal from ourselves the fact that, without the haze — without the shaping ideas we are continually appealing to “under the table” — those low-level processes are impotent to

explain anything.

The cell is an irreducible complexity. The science of genetics itself — where the autonomous, controlling gene has been rapidly ceding its sovereignty to the almost inconceivably complex interactions of the cell as a whole — is currently bearing out this truth in the most dramatic way. But the cell's wholeness, this irreducible complexity, need not be seen as an unapproachable mystery. Organic form is something we can learn to observe and understand — and even our most minutely focused investigations can help us toward this end. It requires only that we let go our fixation upon faux-materialistic concepts and accept the language of form and of organic unity that our explanations already surreptitiously draw upon.

10 The Limits of Natural Selection

The wonder we feel when standing before the more striking and enigmatic examples of biological form is, then, a wonder appropriate to *all* manifestations of biological form. None of them can be — none of them *needs* to be — explained by genetic, physiological, or mechanical “causes” — although such would-be explanations add valuably to our understanding insofar as we learn the language of form and gesture that illuminates and raises to coherent wholeness the observed details we are focusing on. Unlike with the attempted reduction to mindless mechanisms, which in effect tries to *explain away* the intelligible, expressive, evocative realities of form, true understanding of form does not remove our sense of wonder, but only deepens it.

But it's not only the development of form in the individual organism that is obscured by the usual explanations. The same problem occurs when we confront the phylogenetic (evolutionary) elaboration of form. The evolutionary question, of course, was Darwin's main concern when he worried about the eye or the peacock's feathers. But he should have worried about much more than those particular features, for in this domain, too, we find the explanatory gap in more than just a few exceptional cases; it vitiates all attempts to understand organic form as a result of natural selection.

Any form we actually find in a plant or animal must have been able to survive — that's clear enough, even if slightly on the trivial side. And, given two or more variant forms, we can try to identify some of the factors that might have favored one of them over the others. But first the forms need to be *given*. As Portmann puts it when talking about animal forms: natural selection “might afford a reason for their preservation, but never provides the cause for their origin” (1967, p. 23). There is nothing in the “mechanisms” of natural selection — no more than in genetic switching networks — that can specify or characterize form. Even if we think (misleadingly) of natural selection as “guiding” the organism toward fitness, this is a guidance in terms of functional effectiveness, not in terms of form. If we find recognizable forms in the world, *what* we are recognizing — as opposed to its practical utility — cannot be explained through natural selection. Some may want to hand the form itself over to pure chance, but in light of the centrality of form in biology, this amounts to a dismissal of the possibility of a biological science.

The world presents us with aesthetically noteworthy biological forms on every hand —

you could almost say that the biologist faces *nothing but* such forms — and for the vast majority of them no one has ever dreamed of finding an explanation based on natural selection. Just think of the endless diversity of leaf shapes, each a distinctive organic unity with its own recognizable character, and yet no one suggests that all these different shapes have been produced by selection pressures stemming from, say, feeding insects. And in countless other cases the coloration, design, and overall form of an organism (for example, some of the patterns on sea shells) are not even visible to other creatures — not, at least, in any way that might bear on survival — yet “this does not exclude vividly colored patterns, or shapes which appear beautiful to our eyes” (Portmann 1967, p. 113).

The biologist does possess what Portmann calls a “curio cabinet” containing various examples of protective coloration, warning coloration, mimicry, and the pollination of flowers by insects and other organisms. These cases certainly point to a legitimate role for natural selection. But after we have identified the utility of some trait, the specific form itself remains to be accounted for. Why *this particular pattern* for performing the function, when an infinite variety of other patterns could achieve the same thing? The specific form of a bird’s feathery crest or a butterfly’s wing, the shape of antlers or horns, the patterns on a zebra’s head “are by no means explained” by the function (Portmann 1967, pp. 208–9).

Every organism “speaks itself into the world” as a unity of expressive form. That’s what we see. And we will never understand a unified form by talking about how its parts are tinkered together. We have to find a language that matches the phenomena we observe. In every organism we see parts that are themselves expressions of the form of the whole. In our attempts to understand, we cannot escape the language of form, so we might as well start learning how to use this language in an accurate and revelatory way.

11 Biology Without the Cold Shudder

Our trouble today is that we can’t believe what we observe — just as Huxley could not take with full seriousness the artistic sculpting of the embryonic newt playing out beneath his fascinated gaze. Living in a thoroughly Cartesian age, he could not accept the idea *in nature* — the idea that made the proceedings he witnessed through the lenses of his microscope such a compelling drama — and therefore he was forced to slough this idea off, at least rhetorically, upon an external artist, the equivalent of today’s Intelligent Designer.

In the same way Darwin, hearing the suggestion that natural phenomena are the “effect and expression of Mind,” couldn’t help feeling himself forced to choose between an external, “interfering” Mind and the evident continuity of the physical processes he had spent a lifetime observing. The choice in favor of what he conceived as mere physical process would have been less painful were it not for the fact that what he, like Huxley, was observing all this time was a drama of developing form. So only with difficulty could he banish altogether from his awareness the “invisible artist” whose work he was continually witnessing.

In a less dualistic age the Duke of Argyll (and with him the theologians) might have realized that any Divinity worthy of the title must be not only transcendent, but also immanent, working *from within* the depths of physical process — and, further, that the transcendence must not be thought to contradict the immanence. Darwin, in turn, might have realized that to acknowledge phenomena as the qualitative expressions of mind does not require us to suppose an interfering agency. We can freely grant the evident mind-like character of the world, which always presents us with significant form, and this in no way threatens the integrity of scientific knowledge.

When we truly see — that is, when we see with *understanding* — what we see are phenomena bathed in the aesthetically satisfying light of reason. We see ideas so meaning-rich, so manifold, so intimately interwoven with one another, that they can manifest materially only as imaginal forms. These forms are what nature is. To understand a phenomenon of nature means to apprehend its forms and trace them as exhaustively as possible through all levels of their physical manifestation until the picture stands complete before us. A great deal of scientific work serves this purpose admirably — or would do so if only we paid attention to *all* our cognitive activity.

The scientist who does give this kind of attention to nature will be rid once and for all of the cold, Darwinian shudder, exchanging it for the inestimable delight of discovery — discovery, within his own imagination, of the imaginal powers shaping the world before his very eyes.

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