1 On Transmuting Boyle's Law to Darwin's Revolution

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Adaptive continuity

Perhaps there will not always be an England (particularly on time scales favoured by palaeontologists), but a few miles of Channel and nearly a thousand years of freedom from full-scale invasion (1066 and all that) have produced a plethora of British distinctions, both idiosyncratic and deeply philosophical, from continental preferences and modes of thought. (A common language across 3000 miles of ocean can inspire more closeness than twenty miles of *La Manche* accompanied by a divergence of tongues – hence the similarities between American and British histories of evolutionary thought, as discussed in this article.) In this work, I try to identify adaptation as the most distinctly anglophonic subject of natural history and subsequent evolutionary ideas. I set out to show that Charles Darwin's (Figure 1) decision to site his defence and mechanism of evolution in the explanation of adaptation has roots in a long tradition of English natural history and theology that never provoked much continental attention. Our current struggles over 'ultra-Darwinian' versus structuralist modes of thought continue the same debate and establish a particularly English continuity across several centuries.

In the operative paragraph of his Introduction to *The Origin of Species*, Charles Darwin stated (1859, p. 3) that the classical subjects of natural history could provide sufficient evidence for the factuality of evolution:

> In considering the Origin of Species, it is quite conceivable that a naturalist, reflecting on the mutual affinities of organic beings, on their embryological relations, their geographic distribution, geological succession, and other such facts, might come to the conclusion that each species had not been independently created, but had descended, like varieties, from other species.

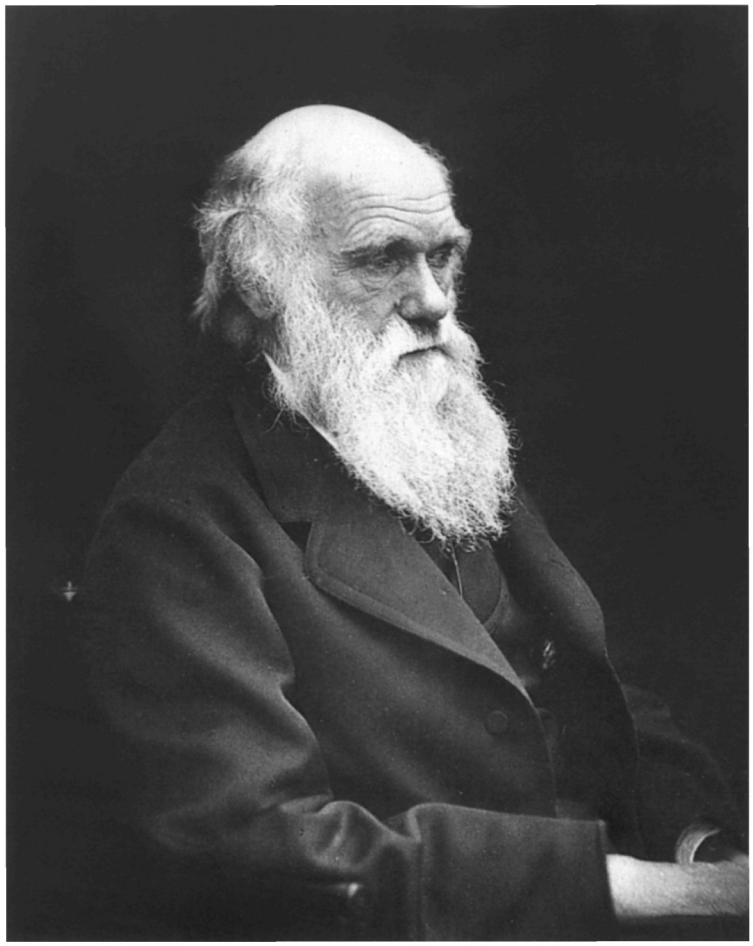

FIGURE 1 Charles Darwin, by Leonard Darwin (1878).

He then added, in a portentous line that has sounded throughout the subsequent history of evolutionary theory, that such an explanation would seem empty, not only for leaving out a central subject, but on aesthetic grounds as well:

> Nevertheless, such a conclusion, even if well founded, would be unsatisfactory, until it could be shown how the innumerable species inhabiting this world have

> been modified, so as to acquire that perfection of structure and coadaptation which most justly excites our admiration.
>
> (*Ibid.*)

Darwin then cites his reasons for locating the causes of evolutionary change – not just its factuality, which can be otherwise ascertained – in both the *complexities* and *precision* of good organic design (and not just the simple existence thereof). Darwin invites us to consider the alternatives: how else, other than by natural selection, might precise adaptation arise by material causation rather than direct supernatural construction? Darwin notes that environmental induction of variation would be cited by most evolutionarily inclined naturalists, but such an explanation cannot account for the complexity and beauty of adaptation (an argument with a strong aesthetic component):

> Naturalists continually refer to external conditions, such as climate, food, *etc.*, as the only possible cause of variation. In one very limited sense, as we shall hereafter see, this may be true; but it is preposterous to attribute to mere external conditions, the structure, for instance, of the woodpecker, with its feet, tail, beak, and tongue, so admirably adapted to catch insects under the bark of trees.
>
> (*Ibid.*)

Add the Lamarckian notion of use and disuse (which Darwin labels 'habit') or direct organic will (his standard misreading of Lamarck, taken in part from Charles Lyell's summary in volume two of the *Principles of Geology* (1832)), and one might edge closer to an explanation for precision, but not for intricate coadaptation between ecologically interdependent organisms. Darwin continues (1859, p. 3):

> In the case of the misseltoe, which draws its nourishment from certain trees, which has seeds that must be transported by certain birds, and which has flowers with separate sexes absolutely requiring the agency of certain insects to bring pollen from one flower to the other, it is equally preposterous to account for the structure of this parasite, with its relations to several distinct organic beings, by the effects of external conditions, or of habit, or of the volition of the plant itself.

We are left with only one alternative to natural selection: the orthogenetic notion of a 'pre-programmed' sequence of phylogenetic transformation, as the Scottish author and publisher Robert Chambers advocated in the anonymously published *Vestiges of the Natural History of Creation* (1844). Darwin properly

rejects this notion on methodological grounds – as entirely untestable in the same sense that creation by divine fiat can never be proven and cannot therefore be regarded as useful:

> The author of the 'Vestiges of Creation' would, I presume, say that, after a certain unknown number of generations, some bird had given birth to a woodpecker, and some plant to the misseltoe, and that these had been produced perfect as we now see them; but this assumption seems to me to be no explanation, for it leaves the cause of the coadaptations of organic beings to each other and to their physical conditions of life, untouched and unexplained.
>
> (Darwin, 1859, p. 4)

English-speaking evolutionists are so accustomed to accepting the primacy of adaptation that they tend to regard such paramountcy as self-evident and not subject to alternative construction. But a decision to view adaptation as the central phenomenon for evolution to explain represents a peculiarly English strategy, and by no means a universal approach. Darwin's revolution may be defined by its radically new and utterly inverted explanation of adaptation, but not by a decision to make the subject central – for good design had been the primary subject of English natural history for at least 200 years.

These differences in national styles, since they began long before the acceptance of evolutionary perspectives, arose from varying approaches to the question of how the workings of nature might reflect the presence and attributes of a divine creator. The distinctively English tradition of 'natural theology' held that God's existence, and also his attributes of goodness and omniscience, could be inferred from the excellence of organic architecture, particularly the good design of organisms and the harmony of ecosystems. Natural theology was defended by some of the greatest seventeenth-century scientists in Newton's orbit, Robert Boyle and John Ray in particular; achieved a culminating statement in the immensely influential *Natural Theology* of William Paley, first published in 1802; and enjoyed a final exuberant fling, a bit past its time perhaps, in the sequence of Bridgewater Treatises published during the 1830s. The natural theologians therefore viewed 'adaptation' – their word, by the way, not Darwin's invention or evolution's neologism – as the primary phenomenon of biology because God's existence and nature lay best revealed therein.

Such an attitude would have seemed peculiar to most continental biologists who did not (of course) deny adaptation, but who tended to view good design as a set of superficial and particularistic tinkerings upon the basic illustrations

of divine intelligence: underlying structures, and the patterns of their transformation in the taxonomic ordering of animals. Most continental structuralists viewed a well-webbed duck's foot, or a good-digging mole's forearm, as too singular and too puny to illustrate something so ineffable and general as God's omniscience. Louis Agassiz, for example, the great Swiss (and, later, American) zoologist of Darwin's generation, and the last major scientific creationist, held that the taxonomic structure of the animal kingdom best revealed God's nature and intentionality – for each species is an incarnated thought in God's mind, and relations among species therefore display the character of God's mental machinery.

I do not mean to cast this distinction as a pure and invariant dichotomy. Some continentals, notably the French naturalist Georges Cuvier himself, maintained a predominantly adaptationist outlook (non-evolutionary, of course, for Cuvier). And some Englishmen favoured the search for geometric rules of archetypal transformation over a singular focus on adaptations, each separately fitted to a particular environment – including Richard Owen, whose adherence to this unfamiliar style of evolutionism led to his frequent misinterpretation (abetted by a growing Darwinian establishment, quite content to malign their principal enemy) as a lingering creationist (for non-adaptational evolutionism might easily be misread as a denial of the entire theme, rather than only of centrality for Darwin's favoured phenomenon). Paleyan natural theology may have been more the preserve of dons and divines in Cambridge than of the medical radicals in Edinburgh and London (who, as the biographer and historian of science Adrian Desmond has shown so well, often embraced Lamarckian and structuralist views); but Darwin ran with the Cambridge crowd, and this strand of intellectual genealogy ultimately prevailed in British biology.

I therefore consider it useful to examine the distinctively British continuity between the adaptationism of the natural theologians and its transmogrification into Darwin's world of descent with modification. The contrast has often been drawn between Paley and Darwin – and fairly enough, for the essence of Darwin's revolution may be defined by the causal inversion thus introduced – but few have focused on the equally striking continuity. Darwin, in short, kept the phenomenology and inverted the explanation – and we need to understand the part retained as well as the portion overturned.

Natural Theology has usually been characterized by its late and canonical

expression in Paley (or by its death throes in the later Bridgewater Treatises). I would rather focus on the founding documents of Newton's age – particularly on my favourite work by the greatest of Newton's contemporaries who treated the subject explicitly and at length – Robert Boyle, in his 1688 work entitled *A Disquisition About the Final Causes of Natural Things, Wherein it is Inquir'd Whether, and (If at All) With What Cautions, a Naturalist Should Admit Them.* I want to examine how Boyle sets up the argument for organic adaptation as the primary natural clue to God's existence and attributes. I shall then discuss the features of his system that persist with most continuity into later Darwinian traditions, and also the components most radically overturned by evolutionism. In tracing this unbroken thread, I believe that we can also best understand the differences. As for the lineages of organisms that he studied in nature, Darwin's theory emerged in genealogical continuity with a local intellectual ancestry. We will best understand the truly revolutionary aspects of natural selection when we can map its explanatory inversion upon the unaltered conviction that adaptation represents the central phenomenon requiring explanation by any adequate theory of life's history.

Boyle's formulation

The architects of the scientific revolution (that is, the late seventeenth-century formulation of modern science that historians tend to dignify, often in upper case, as *The* Scientific Revolution) held a distintive attitude towards the role of God in nature. All were devout theists, perhaps no one more so (or at least in a seriously conventional manner, for Newton certainly had maximal zeal) than Robert Boyle (Figure 2). They did not deny to God his traditional prerogative of miraculous interference into the affairs of nature, whenever he so desired or felt the need. Boyle, for example, writes in his *Disquisition* (1688, p. 96):

> Nor is this doctrine inconsistent with the belief of any true miracle; for it supposes the ordinary and settled course of nature to be maintained, without at all denying, that the most free and powerful author of nature is able, whenever he thinks fit, to suspend, alter, or contradict those laws of motion, which he alone at first established, and which need his perpetual concourse to be upheld.

But in general, and effectively all the time, God will not so intervene. A deity who must perpetually put his finger into nature's affairs, to correct some glitch that his own omniscience should have foreseen, is a poor and bumbling power

FIGURE 2 Robert Boyle.

indeed. How much more majestic to posit an infallible God who ordains all laws at the inception of the universe to produce the desired effects throughout later history and without further direct maintenance. 'This doctrine' (to use Boyle's words) of a 'clockwinder' God, who got the laws right at the beginning and thereafter let nature run by the invariant principles that he had ordained, forged a beautiful harmony between serious belief and untrammelled science – for God, as a perfect mechanic, combines maximal majesty with minimal per-

turbation. In short, the author of nature had made a world that science might fully comprehend.

But such an operational attitude entails a paradox. If 'the heavens declare the glory of God; and the firmament showeth his handiwork' (recall Haydn's setting of these words in his oratorio *The Creation* (1798) when you envisage the emotional power of this claim), then how shall we know this most fundamental of all truths? If nature now operates by invariant laws, where is God's imprint upon the works of his creation? No doubt he ordained the inverse-square law, but such mathematical abstractions seem a bit distant from our need to affirm his benevolence and his loving kindness towards humanity, the crown of his creation. How shall we know our favoured status? How shall we remain sure that 'though after my skin worms destroy this body, yet in my flesh shall I see God' (and now think of Handel's setting in *Messiah* (1741)).

The most attractive resolution of this paradox lay in the old Aristotelian doctrine of final cause. (Remember that Aristotle, in the *Organon*, divided causality into four distinct modalities, which he named material, efficient, formal and final. Using the familiar 'parable of the house', the standard pedagogical device for explicating this notion, material causes are the stuff of construction – straw, sticks and bricks offering different degrees of protection against wolves, for example. Efficient causes are the actual 'hands-on' makers of the effect – the mason who lays the bricks. Formal causes are the abstract plans or archetypes that govern the construction; blueprints do not make anything directly, but you will not progress beyond a pile of bricks without such a planned design. Final causes are purposes, for the house will not be built unless someone wants to live there and can commission the builders for this end.)

The scientific revolution placed such primacy upon efficient causes that modern usage has restricted the entire concept to only one of Aristotle's four modalities. We still acknowledge the importance of material and formal factors, but we no longer refer to them as causes. Final causes have been banned for inorganic objects (the moon does not exist to illuminate the night sky), and accepted as an unintentional consequence of natural selection in the evolution of organisms (moles do have stout forearms for digging, but they did not consciously strive to evolve such structures). The human brain grants us intentionality and final cause in the original sense, but we are in oddity in nature.

Final cause, however, remained a legitimate notion for scientists of Boyle's generation (despite Francis Bacon's famous deprecation). For Boyle, final cause

could act in a realm parallel to the efficient mechanisms of his clockwork universe. Efficient causes pushed all the springs and cranked all the pulleys, but final causes expressed the purposes that God had in mind when he ordained the efficient mechanisms of his clockwork universe. God need not show his hand by miraculous intervention into the realm of efficient causation; Boyle's God is manifest in the final causes of phenomena constructed by ordinary efficient causes under nature's invariant laws.

But which phenomena of nature are best suited to the discovery and elucidation of their final causes? The logic of Boyle's presentation leads us squarely to organisms and their good design – in short, to adaptation as the quintessential natural phenomenon for displaying God's existence and attributes. In the *Disquisition* Boyle begins by citing the two major philosophical opponents to final causation: the Epicurean belief that a random universe can manifest no purpose, and the Cartesian claim that God's ends are too ineffable for human comprehension:

> Two of the chief sects of the modern philosophers, both of them, though upon differing grounds, deny that the naturalist ought at all to trouble or busy himself about final causes. For Epicurus, and most of his followers . . . banish the consideration of the ends of things; because the world being, according to them, made by chance, no ends of any thing can be supposed to have been intended. And on the contrary, Monsieur Des Cartes, and most of his followers, suppose all the ends of God in things corporeal to be so sublime, that 'twere presumption in man to think his reason can extend to discover them. So that, according to these opposite sects, 'tis either impertinent for us to seek after final causes, or presumptuous to think we may find them.
>
> (*Ibid.*, Preface)

Boyle then structures his search as a 'Goldilocks' problem, an attempt to find the 'just right' phenomenon between two extremes. He proposes three categories of natural objects that might manifest final causes: inanimate bodies of the cosmos, inanimate objects on earth and organic bodies on earth.

As the 'too big' category that will not illuminate final cause, Boyle identifies the immense cosmic bodies of the universe. Suns and planets must have divine purposes, but here Descartes may well be right, for we tiny inhabitants of one little planet will not be able to read God's purposes at so grand a scale. Cosmic bodies certainly show God's glory, but not his beneficence and care for us. 'The Cartesian way of considering the world, is very proper indeed to show the

greatness of God's power, but not, like the way I plead for, to manifest that of his wisdom and benevolence' (*ibid.*, p. 37).

Into the 'too small' category of phenomena beneath God's adequate glory, Boyle places the inorganic phenomena of our scale on earth. For these bodies are too simple, and could well be formed either by chance as the Epicureans say, or by simple assembly following invariant laws of nature (God made the laws, of course, but final causes should illustrate his glory directly, not by one removal):

> As for other inanimate bodies, as stones, metals, *etc.*, whose matter seems not organized, tho' there be no absurdity to think, that they also were made for distinct particular purposes . . . yet most of them are of such easy and unelaborate contextures, that it seems not absurd to think, that various occursions and jostlings of the parts of the universal matter may at one time or another have produced them.
>
> (*Ibid.*, p. 44)

Boyle then nominates animals and plants as the 'just right' category for displaying the final causes that will illustrate God's existence and attributes to us – in other words, as the favoured objects of natural theology. Boyle cites three major reasons for this preference. First of all, organisms are so complex that we cannot attribute their forms and behaviours either to chance or to simple construction by nature's laws without overt and particular purpose:

> There are some effects, that are so easy, and so ready, to be produced that they do not infer any knowledge or intention in their causes; but there are others, that require such a number and concourse of conspiring causes, and such a continued series of motions or operations, that 'tis utterly improbable, they should be produced without the superintendency of a rational agent, wise and powerful . . . I never saw any inanimate production of nature, or, as they speak, of chance, whose contrivance was comparable to that of the meanest limb of the dispicablest animal: and there is incomparably more art expressed in the structure of a dog's foot, than in that of the famous clock at Strasburg.
>
> (*Ibid.*, pp. 45–7)

Second, organisms exist at our scale, and operate much as we do – so we can readily grasp the final causes of their design (as we may not for immense and fiery bodies so distant from the earth as other suns). Boyle focuses his attention on the classic case of adaptation: the design and function of eyes:

> The great author of things . . . has furnished various species of animals with

> organs of sight that are very differingly framed and placed . . . This diversity nobly manifests his great providence, and (if I may so call it) forecast, that has admirably suited the eyes of the differing kinds of animals, both to the rest of their bodies and . . . to those parts of the great theater of the world on which he designs that they shall live and act.
>
> (*Ibid.*, pp. 58–9)

Third, as also illustrated in the quotation above, we can readily grasp the *utility* of organic form and function – and final causes are most clearly manifest in function, or adaptation. Boyle follows the strategy, classic ever since among adaptationists of either creationist or evolutionary persuasion, of discussing apparent exceptions – features that seem degenerate or devoid of function – and then showing that these parts, as well, are optimally suited for a creature's particular mode of life. Boyle discusses the rudimentary eyes of moles:

> The eyes which nature hath given them, are so little, in proportion to their bodies, that 'tis commonly believed, and even by some learned men maintained, they have none at all. But though by anatomy, I, as well as some others that have tried, have found the contrary; yet their eyes are very differing from those of other four-footed beasts. Which is not to be wondered at; considering, that the design of nature was, that moles should live under ground, where a sight was needless and useless; and where greater eyes would be more exposed to danger: and their sight, as dim as 'tis, is sufficient to make them perceive that they are no longer under ground, . . . which seems to be the most necessary use they have of light and eyes.
>
> (*Ibid.*, p. 60)

Substitute natural selection for God's foresight, and a Darwinian adaptationist would not formulate the argument about function much differently.

The continuity in adaptation between Boyle's natural theology and Darwinism

With many exceptions to be sure, organisms do tend to be well designed, and though Darwin inverted Boyle's explanation, the phenomenology endures. Consequently, the power of the adaptationist programme remains unchanged from Boyle to modern Darwinism – as seen most clearly in the eminently operational and highly fruitful strategy of assuming good operation 'for' some function when trying to analyse an enigmatic structure. Boyle's brilliant passage on how William Harvey used the structure of venal valves to infer circulation of the blood beautifully illustrates Louis Pasteur's famous quip that 'fortune fav-

ours the prepared mind', and illustrates how assumptions of good design can work as admirable preparation. Substitute 'natural selection' for 'so Provident a Cause', and the heuristics of modern adaptationism shine forth just as well in this passage. Modern defenders of adaptationism (see, for example, Ernst Mayr's article for *American Naturalist*, 1983) locate a primacy rationale in the same utilitarian argument:

> I remember that when I asked our famous Harvey, in the only discourse I had with him, (which was but a while before he died) what were the things that induced him to think of a circulation of the blood? He answered me, that when he took notice that the valves in the veins of so many several parts of the body were so placed that they gave free passage to the blood towards the heart, but opposed the passage of the venal blood the contrary way: he was invited to imagine that so provident a cause as nature had not so placed so many valves without design: and no design seemed more probable than that, since the blood could not well, because of the interposing valves, be sent by the veins to the limbs; it should be sent through the arteries and return through the veins, whose valves did not oppose its course that way.
>
> (*Disquisition*, pp. 157–8)

But just as the method works so powerfully when the mechanics of good design can be thus exposed, notable foibles and weaknesses appear (for Boyle in 1688, as for adaptationists today) when the presumption of optimal function becomes a dogma asserted *a priori*, and a claim irrefutable in principle. The two most frequent critiques of uncritical and overextended adaptationist arguments today may also be applied to several of Boyle's examples, thus establishing a continuous pedigree across this greatest of intellectual divides, from creationist to evolutionary biology.

'Just so stories', with cleverness, rather than empirical support, as a primary criterion

Harvey's functional argument triumphed both because he could obtain confirming evidence (and could use his fruitful hypothesis to direct the search), and because he was right in his claim. In other and opposite uses – tactics that stymie investigation rather than inspire testing – adaptationists, all too frequently, simply propose a cunning explanation, and then consider their work accomplished by cleverness of argument, rather than empirical validation of claims. Many critics have referred to these proposals as 'just so stories', invoking

Rudyard Kipling's purposely fanciful explanations of how elephants got long trunks, and rhinoceroses wrinkled skin.

Consider a sequence of Boyle's claims in this mode, moving from the potentially valid to the demonstrably false. All fall into the pre-eminent category of adaptationist puzzles – structures that seem ill designed or devoid of function, but that none the less require adaptive explanation if the paradigm be as universally valid as supporters desire:

(1) *For transient non-utility*: How can a functional argument be constructed for embryonic structures that appear only transiently, and have no known intrauterine function. Boyle makes the clever argument, probably correct in this case, that such features are structural prerequisites (he calls them 'scaffolds') for the functioning organs that will follow:

> 'These temporary parts were framed by a forecasting, as well as a designing, agent, who intended they should serve for such a turn, and then be laid aside; it being utterly improbable, that an undesigning agent should so appositely and exquisitely frame scaffolds for the future buildings, if he did not beforehand destinate both the one and the other, to concur to the same ultimate effect.'
>
> (*Ibid.*, p. 167)

In this case, we must also recognize that, to Boyle and his contemporaries, a documentation of adaptive value for some future state – scaffolding for the later building – seemed a particularly powerful argument for a conscious designer: for how else could a structure arise only to bolster later utility? Our age has found a different solution in the concept of programmed instructions and their evolution. But Boyle's generation scarcely possessed even a metaphor for such a notion, except, perhaps, in toys like the music box. The introduction of the Jacquard pattern weaving loom in the eighteenth century, and of computer technology in our own times, has made this concept among the most familiar in modern life. We can all grasp the workings of DNA, and no scientist would now claim that organic construction for future ontogenetic utility implies anything about conscious design.

(2) *For apparent redundancy*: Moving to the less plausible though not ridiculous, and still entirely in the speculative mode, Boyle completely ignores the obvious structuralist alternatives and argues for a purely functional explanation of bilateral symmetry as insurance against loss:

> 'There seems to have been care taken, that the body of an animal should be furnished, not only with all things that are ordinarily necessary and convenient, but with some superabundant provision for causalities. Thus, tho' a man may live very well, and propagate his kind, (as many do), tho' he have but one eye; yet nature is wont to furnish men with two eyes, that, if one be

destroyed or diseased, the other may suffice for vision . . . In short, nature has furnished men with double parts of the same kind, where that duplicity may be highly useful.'

(*Ibid.*, p. 143)

(3) *For apparently overt harm:* Boyle argues, exposing another and still pervasive aspect of cultural bias in the ranking of our genders, that the anatomical weakness of a woman may not be 'good' for her individual life, but benefits the species as a whole in aiding procreation:

'Those of the female sex are not so happily framed, in order to their own welfare, as those of the masculine: since the womb, and other things peculiar to women, which are not necessary to the good of individual persons, but to the propagation of their species, subject that tender sex to a whole set of diseases, belonging to them either peculiarly, as they are women, or as they are with child, or brought to bed; from all which men are exempt . . . Men [*now meaning all people*] may sometimes mistake, when they peremptorily conclude, that this or that part of an animal must, or cannot, have been framed for such an use, without considering the cosmical, and therefore primary and over-ruling ends, that may have been designed by nature in the construction of the whole animal.'

(*Ibid.*, p. 220)

(4) *Guesses that turn out to be just plain wrong*: This general tactic suffers most when later discovery exposes earlier proposals as no more than fatuous guesswork. The last quotation provides one example, for we now know that women exceed men in life expectancy – so Boyle's 'sure' knowledge of divine intent suffers inversion. As another example, cleaner for exposing foibles of the method, though clearly of much less social import – Boyle apparently thought, quite wrongly, that human teeth continued to grow throughout life, and he proposed divine utility for this non-existent phenomenon:

' 'Tis considerable, that whereas, when man is come to full stature, all the other bones of the body cease to grow, the teeth continue to grow in length during a man's whole life . . . Of the difference in point of growth betwixt the teeth and other bones, what reason can be so probably given, as, that 'tis designed to repair the waste that is daily made of the substance of the teeth, by the frequent attritions that are made, between the upper and lower tier in mastication.'

(*Ibid.*, p. 182)

Switching only within the paradigm upon falsification

Critics would not object so strongly to adaptationist arguments as invariable first approaches if falsification of a particular claim could lead to tests of truly different alternatives outside the adaptationist programme. But the committed

functionalist does not work in so open a manner, and disproof of one adaptationist hypothesis leads only to lateral feinting towards a different story, still invariably in the functional mode. Thus, the paradigm cannot be refuted from within.

We already encountered one example of this 'unbeatable' strategy above, when Boyle, puzzled by the supposed bodily weakness of women, and meeting difficulty in contriving a functional argument based on advantages for individual women, simply switched levels within the paradigm by arguing that any detriments to women as individuals must be outweighed by benefits accruing to the entire species.

Boyle uses this tactic throughout his exposition. After praising the ubiquity of good biomechanical design, for example, Boyle falters when he cannot find a functional explanation for vibrant animal colours (ironic, since we have now taken most cases into the paradigm under the guise of sexual selection). But he does not abandon functional explanation; instead, he switches, arguing that colours must be 'for beauty', rather than biomechanical utility:

> It may help us if it be considered, that, since God is both a most free and a most wise agent, it need not seem strange that he should adorn some animals, with parts or qualities that are not necessary to their welfare, but seem designed for their beauty: such as are the disposition of the camelion to change colours; and the lovely greens, blews [*sic*], yellows and other vivid colours that adorn some sorts of pigeons, and of parrots . . . and especially those admirable little winged creatures humming birds.
>
> (*Ibid.*, p. 205)

Extending the same argument to the even more troubling fact of riotous diversity upon common designs (why do so many kinds of eyes exist, when the basic structure works so well, and when most variants have no obvious link to particular modes of life), Boyle floats the peculiar proposal – and do I, for once, detect just a trace of timorousness on his part for the 'reach' of his special pleading – that God uses this variety to instruct us about the range of His wisdom. (I find this argument all the more forced because ordered diversity not linked to particular life styles provides the strongest phenomenology for the alternative structuralist approach based on 'laws of form' and the regularities of transformation):

> If that be admitted . . . as very likely, that God designed, by the great variety of his works, to display to their intelligent considerers, the fecundity (if I may so

> speak) of his wisdom; one may readily conceive that a great part of the variety observable in the analogous parts of animals, as their eyes, their mouths, *etc.* may be very conducive to so reaching and comprehensive a design; to which the beauty of some creatures and parts, as well as their more necessary or convenient structure, may be subservient; especially if the innocent delight of man be also intended, as it may seem to be in the curious colours and shapes of divers flowers, and in the melodious musick of singing birds, and in the vivid and curiously variegated colours of the feathers of several winged animals, particularly those that make up the peacock's train.
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> (*Ibid.*, pp. 208–9)

To end this section with Boyle's most explicit affirmation of exclusive adaptationism as a methodology, he defends both tactics critiqued above – reliance on conjectural 'just so stories', and switching only within the paradigm upon refutation of particulars – by stating that we poor mortals cannot grasp the full range of God's intent, and that our failures to discern function point more surely to our ignorance than to the propriety of an alternative explanation:

> Men may easily be too rash, if they think a part bunglingly framed, upon supposition that, by the anatomical inspection of it, they know all the uses that the skill of the divine opificer could design for it.
>
> (*Ibid.*, p. 203)

> Tho' we may safely conclude that God acts wisely, when he does something that has an admirable tendency to those ends we justly suppose him to have designed; yet we cannot safely conclude in a negative way, that this or that is unwise, because we cannot discern in it such a tendency. For so wise an agent may have other designs than we know of, and further aims than we can discern or perhaps suspect . . . [aims that are] far above the reach of our conjectures, and without the knowledge of which we but rashly censure the wisdom of his proceedings.
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> (*Ibid.*, pp. 209–10)

A truly unbeatable argument but, for that reason (or so we would say today), not very useful in science!

The radical difference between created and evolutionary (particularly Darwinian) adaptationism

Darwin frequently stated that he had tried to advance two quite separate innovations in proposing his theory of 'descent with modification': first, simply to

convince people of evolution's factuality (implying the genealogical basis of organic relationships and the transmutational interpretation of life's history); and, second, to propose a theory (natural selection) for the causes of this factuality. He then added that the first aim – establishment of factuality rather than confirmation of mechanism – must be viewed as far more important because the revolutionary consequences of such an admission ran so deep and so counter to Western traditions. We may use this famous, and wonderfully perceptive, self-assessment to identify what changes so radically amidst the continuity of adaptationist argument in anglophonic natural history.

Beginning with the second aim of establishing theory, many historians have noted that the most revolutionary feature of Darwin's mechanism lies in its almost brutal inversion of natural theology. For Boyle, adaptive design represents the direct handiwork of a caring God; for Darwin, the same phenomenology emerges as a side-consequence of a causal principle that could carry only opposite moral messages, if morality could be read in nature (as, according to Darwin, it most definitely cannot) – namely, a struggle among individual organisms for personal reproductive success.

This crucial inversion imposes a difference in the manner of adaptationist argument pursued by Boyle and later Darwinians – for Boyle may locate adaptation at any level of biological organization (as all can display God's intent), while Darwin must ascribe benefits only to organisms in their reproductive competition, and must therefore deny such 'cosy' concepts as the 'good of the species'. Boyle, as we have seen in his argument about the supposed weakness of women, happily switched to adaptive benefits for entire species when he could not identify advantages for individuals. In an even more telling example, Boyle recognizes the placenta as excellent design, but can only attribute the structure to divine beneficence for our entire species, since the health and strength of individual women are not enhanced thereby (and Darwin's key notion of individual *reproductive* success as an organic *summum bonum* is understandably absent from Boyle's mental map of nature):

> Those temporary parts appear to have been designed by nature, not so much for the personal preservation of the female as for the propagation of the species: which destination . . . appears to have been preordained by the author of mankind for the continuation of it [that is, the species].
>
> (*Ibid.*, p. 152)

However striking this difference imposed by theory, far more portentous changes were enjoined (as Darwin had correctly noted) in accepting Darwin's first aim of establishing the basic factuality of evolution. After all, Darwin's own insistence upon struggle among individuals as the only proper level for arguments based on natural selection – however brilliantly affirmed in the twentieth-century history of evolutionary thought – was quite idiosyncratic to Darwin, and so radical that most of his contemporaries, including his strongest supporters, never understood the depth of meaning involved in this restriction in levels. Darwin's colleague and co-proponent of the theory of natural selection Alfred R. Wallace, for example, was quite content to make conjectural arguments about natural selection at all levels, including frequent claims about the 'good' of species. Thus, Wallace's evolutionary arguments might not have differed from Boyle's defences for design on this score.

But the simple admission that organisms have histories of genealogical connection imposes such a different geometry upon the structure of life that all arguments in natural history must alter. (This grand change has minimal effect upon claims about good design for *particular* creatures in one environment at *one time* – hence the maximal continuity between Boyle and Darwinism on questions of adaptation.)

At the broadest scale, genealogical thinking opens the insight that many anatomical features must be simple signs of ancestry and need not be elaborately explained, part by individual part, as adaptations expressly crafted for current function. As Boyle struggles to explain why bats, uniquely among 'birds' (used as a functional term for flying vertebrates, not as a genealogical designation), have so many characters otherwise found only in furry creatures on the ground, one almost wants to kick him and say: 'don't you see; it's so simple; bats are mammals by ancestry' – but then, of course, Boyle could not see this solution, and the role of world views in both constraint and facilitation lies beautifully exposed in the example.

> Though bats be looked upon as a contemptible sort of creatures [*sic*], yet I think they may afford us no contemptible argument to our present purpose. For in the heteroclite [*an archaic word meaning anomalous*] animal, you may discern the fecundity of the divine artificer's skill, which has in this formed an animal that flies like birds, and yet is not only unfurnished with feathers but is of a fabric quite differing from that of other birds. And in this little animal we may

> also observe . . . the regard, which the divine artist appears to have to the symmetry of parts, in his animated works, and to their fitness for the places they are to live in or frequent. For the bat, being to act sometimes like a bird, that flies freely to and fro in the air, and on some occasions like a terrestrial animal, such as is that little quadruped a mouse; ought to be furnished with parts suitable to such different destination.
>
> (*Ibid.*, pp. 193–4)

In a more subtle difference on the same point, construction by sequential history, rather than creation in full perfection, immediately resolves a problem that Boyle found quite puzzling (though not insurmountable by his cleverness): how can we interpret a function that has current utility to an organism, but that must be explained as a secondary consequence of a different primary or original usage – the thin coin minted for currency, but employable as a screwdriver in moments of need. Boyle, lacking a concept of historical change, has to argue that his excellent divinity also foresaw *all* the secondary utilities when he created the feature for a primary role:

> I have seen, and been master of a telescope, made in the form of a walking-staff, so that it was fitted to serve for several purposes; whereof tho' one was very different from the other, yet all of them were in the idea of the artificer, and intended by him.
>
> (*Ibid.*, p. 99)

Think of the intellectual liberation supplied by the stunningly simple alternative that adaptations evolved for one function may be fortuitously fitted to work in other ways as well – so that feathers arising as thermoregulatory devices may then be co-opted for flight. Liberating, but immensely threatening (and therefore invisible for Boyle) to a belief in a young and static world, replete with final causes displaying the existence and benevolent intent of an omnipotent deity.

The importance of conceptualizing alternatives

From my extensive quotation of Boyle, and with the benefit of our Darwinian insight and hindsight, we can easily perceive the confines of his seventeenth-century conceptual prison. Boyle's natural world contains no historical dimension, and he must therefore view every mammalian feature of a bat as expressly created for a current function, and not as a mark of ancestry. His view of nature proclaims ubiquitous purpose (illustrating God's benevolently creative order),

and he must therefore be stymied (or driven to forced conjecture) by a range of phenomena differently and properly rendered in systems ordered by genealogy (features co-opted for secondary functions, vestigial organs, utilities based on criteria – particularly the Darwinian *summum bonum* of reproductive success – unimportant to Boyle's God).

But we would be traitors to the scholarly imperative of search for understanding if we read Boyle's differences from our view of life as an excuse to bewail his opacity, or as a way to exalt our own sophisticated times against his 'bad old days' (I doubt whether any of us could hold a candle – to cite a metaphor of past technologies – to Boyle's raw intellectual power). Rather, we should read the obvious lesson in intellectual constancy. If such a brilliant man dwelled in a conceptual prison so patent to us today, how are we unwittingly incarcerated in systems of belief that will seem just as ludicrous and easily discarded to our descendants?

By tracing the continuity in anglophonic evolutionary thought between Boyle and modern Darwinism on the crucial subject of adaptation, or functional explanation in general, I wish to suggest that we might profitably examine this ancient preference – for our propensities may be recording equal parts of nature's factuality and our own continuing conceptual prisons.

Alternative approaches to evolutionary theory do exist, often with long pedigrees in largely continental traditions; evolution is not co-extensive with adaptationist preferences in explanation. Adaptation will always be a vital subject in evolutionary thought, for organisms do tend to be well designed, and natural selection is a proven and potent force. But adaptation need not be the fundamental result of evolution's causal workings, the pre-eminent and controlling phenomenon of life's transmutational history. Perhaps the continental perspective is more correct, and most adaptations rank as subsequent, particularistic modifications of underlying structures and as products of their transformational rules and regularities.

This forum is not the place for an extensive compendium, or a long defence, of these alternatives. (As an agnostic on this issue, I would not even be comfortable in presenting such a defence, nor can we fairly depict the issue in such a dichotomous manner at all.) But I do think that a variety of structuralist approaches are now in the ascendancy, thus giving new life to an old division that goes back to the pre-evolutionary version of Geoffroy Saint-Hilaire touting the power of archetypes and laws of form against the non-evolutionary

adaptationism of Georges Cuvier in their famous debates of 1830 at the Académie des Sciences in Paris. D'Arcy Thompson kept the structuralist vision alive, with an explicitly anti-Darwinian evolutionary version, in the finest work of prose in English natural history – *On Growth and Form*. This decade, Stuart Kauffman and Brian Goodwin have both written powerful and provocative, if flawed, modern versions that explore sources of biological order arising from structural rules rather than functional selection. (Kauffman, in particular, has underlined the potentially non-oppositional status of structuralism to Darwinian functionalism, pointing out that his laws of form provide order 'for free' to a selective system that can then modify and add further regularity.) Most spectacularly, our stunning successes in beginning to unlock the genetics of development have proven a depth of structural constraint by homology across the most disparate of complex phyla, particularly arthropods and chordates, in body axes, substrates for the formation of eyes and segmental differentiation. Most amazingly (I had long rooted for such a result after writing *Ontogeny and Phylogeny* in 1977, but never dared really to hope for a positive outcome), it begins to apear that Geoffroy Saint-Hilaire was correct in his homology of the vertebrate body plan to an inverted arthropod design, for homologous determinants of dorso-ventral patterning are indeed reversed in the two phyla. Details can be found in the articles by Y. Sasai *et al.* and S. A. Holley *et al.* in the list of Further reading at the end of the chapter.

In this light, one might ask why an evolutionist should worry about the dogmatism of overly strict adaptationism; will this viewpoint not be swept aside by the successes of modern structuralist thinking, thereby leading all evolutionists to a proper pluralism? Apparently not, and ironically, for strict Darwinian adaptationism – now given the quite appropriate name of 'ultra-Darwinism' by B. Goodwin and N. Eldredge – remains strong in anglophonic evolutionary circles (whether by sheer vestigial weight of an adaptationist tradition dating back to the seventeenth century, or by the attraction so many of us seem to feel for simplistically comprehensive world views, I do not know. I do not think that either power of evidence or strength of argument can be supporting such an exaggerated and one-dimensional theory).

I am not much concerned about the fallacies of ultra-Darwinism within evolutionary biology, for most professionals understand the limitations of such a view only too well – and the current leading exponent, Richard Dawkins, seems to maintain a strict attachment to the creed that can only be called theological. I worry more when practitioners of other disciplines dip into evolutionary

biology, see only this traditional (if superannuated) viewpoint, fall in love with its beguiling simplicity and then make the great error of thinking that they have accurately translated another field into their own.

Thus, for example, the philosopher Daniel Dennett extols the ultra-Darwinian straight and narrow, while a caricature of the true richness of Darwinian functionalism passes as a paradigm for a 'new' discipline self-consciously touting itself as 'evolutionary psychology' (see D. M. Buss, 1995, for a technical account of this field, and R. Wright for a sycophantic 'pop' version). Evolutionary psychologists view themselves as 'sophisticated' about adaptation because they do not argue, as some even more naïve sociobiologists did in the last round of discussion, that all behavioural universals must be adaptively maintained. These new apostles of ultra-Darwinism hold that many universals have become tragically non-adaptive in modern society, but must have been adaptive at their origin on the African savannahs (or wherever) – for natural selection is the cause of evolution and natural selection builds adaptation. Thus, the evolutionary psychologists remain thoroughly ultra-Darwinian in positing an adaptive origin for all human universals – while true alternatives require recognition of the richness of non-adaptative means whereby such universal traits may arise – see S. J. Gould and R. C. Lewontin on the principle of spandrels, and other potent non-adaptive mechanisms that must be largely responsible for the uniquely human utilities of our mental functioning.

Darwin's own position in this continuing debate over so many centuries remains powerfully relevant and of far more than mere historical interest. As a subtle thinker, who knew that the richness of natural history could not yield to one-dimensional explanation, but who cherished the power of his own intellectual issue of natural selection, Darwin both overstressed the anglophonic preference for adaptationism that defined his patrimony, and at the same time, warned against too exclusive a reliance on this single mode. In fact, nothing could call forth more annoyance from this remarkably genial man than the distortion of his theory into a cardboard version that equates natural selection with the exclusivity and omnipotence of Boyle's deity (and, on this ground, I am confident that Darwin would have eschewed ultra-Darwinism). For example, he wrote in near despair for the last edition of the *Origin of Species* (1872, p. 395):

> As my conclusions have lately been much misrepresented, and it has been stated that I attribute the modification of species exclusively to natural selection, I may be permitted to remark that in the first edition of this work,

> and subsequently, I placed in a most conspicuous position – namely at the close of the Introduction – the following words: 'I am convinced that natural selection has been the main, but not the exclusive means of modification.' This has been of no avail. Great is the power of steady misinterpretation.

And yet, Darwin was not a pluralist without preference. His basic world view elevated the functional mode above all others by defining adaptation as the central problem of evolution (see the set of quotations on pp. 4–7). In so doing, he expressed his fealty to a national tradition extending right back to Boyle and his compatriots at the foundation of modern science.

When I last spoke at Darwin College, for the grand celebration held to commemorate the centenary of Darwin's death, I ended my presentation with an incisive line from William Bateson, a great non-Darwinian evolutionist who none the less caught the essence of Darwin's paramountcy among English scientists. As I have written an article about continuity across centuries and through the greatest of all intellectual transformations in the history of biology, may I end with a small personal continuity in citing Bateson once again, and in the same position – for his words ring with the explanatory pluralism that we will have to champion if we wish to fathom the complexities of evolution:

> We shall honour most in him not the rounded merit of finite accomplishment, but the creative power by which he inaugurated a line of discovery endless in variety and extension.
>
> (Bateson, 1909)

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