The following review was earlier published in the 25 May issue (1994, **66**, 798–800). Unfortunately there was an error in the spelling of the reviewer. We are therefore reprinting the review with the correct spelling.

– *Editor*

A natural philosopher

Life Cycles: Reflections of an Evolutionary Biologist. John Tyler Bonner. Princeton University Press, 41 William Street, Princeton, New Jersey 08540, USA. 1993. 209 pp.

Among the generation of biologists who began working about mid-century, John Tyler Bonner, Professor Emeritus of Biology at Princeton University, and author of *Life Cycles Reflections of an Evolutionary Biologist* (Princeton University Press) has been the prime keeper of a flame that few of his contemporaries realized had nearly become extinguished: the vision of an integrated life science, incorporating both development and evolution. During the early part of this century the fields of developmental and evolutionary biology diverged from one another to the detriment of each. The nineteenth century had seen sweeping generalizations about the relationship between development and evolution, ranging from Haeckel's grandiose 'biogenetic law' which held that ontogeny recapitulates phylogeny, to Von Baer's more circumspect and pertinent observation that the more general characters of the large group of animals to which an embryo belongs appear earlier in development than the more distinctive characters. The confluence of Mendelism and Darwinism at the turn of the century set the stage for a new synthesis in biology, but this time there was little place for embryonic development in the unifying framework.

There were several reasons for this. Among the most important was the great influence of the zoologist August Weismann (1834–1914). Weismann raised to the level of principle the fact that, in animals, the germ line is sequestered from the soma, or body tissues, early during development Another component of the emerging synthesis championed by Weismann was the notion that each biological trait was embodied in a separate particle in the germline. Although particulate inheritance of individual traits was soon rejected by sophisticated Mendelians such as Johannsen and Morgan, the latter day notion that all biological characteristics are encoded in a 'genetic program' is a remnant of this view.

The integration of these doctrines into the emerging neo-Darwinist consensus established a mindset concerning the relation between development and evolution that has remained dominant up to the present time: First, natural selection acts on the frequency of genes only insofar as they influence the reproductive success of adult forms Second, 'programmed' events that occur after the germ cells are set aside are straightforward consequences of gene content. Therefore, the *mechanisms* by which gene activities contribute to the form of the adult, while they may be of interest in themselves, are of little consequence to evolutionary theory.

It is an open secret, however, that plants, colonial invertebrates, and fungi all violate Weismann's doctrine of the separation of germline from soma. Moreover, these forms can also display enormous phenotypic plasticity and ecophenotypic variation, blurring the distinction between development and adaptive strategy, and undermining the view that phenotype is genetically programmed in a strict sense. Thus, while the typical organism in life's history and present day diversity is undoubtedly not Weismannian, our species happens to be, and the mainstream perspective on evolutionary and developmental processes has been correspondingly parochial. It is John Bonner's special distinction to have resisted this parochialism in both his experimental work and integrative writings, and in doing so, to have pointed the way out of what a growing number of contemporary developmental and evolutionary biologists see as a crisis in the reigning paradigm.

In the opening chapter of *Life Cycles* Bonner writes: 'I have devoted my life to slime molds.' This statement, characteristically modest and resonant, echoes that of another American philosopher of life cycles, Henry David Thoreau, who, in a horticultural essay in his contemplative work, *Walden*, avowed that 'I was determined to know beans.'

The organism to which Bonner has dedicated his life, *Dictyostelium discoideum*, a 'social amoeba', is decidedly not a Weismannian creature. It is worth hearing, in Bonner's own words, a description of the life cycle of this microscopic and easily ignored soil organism·

> The molds begin as encapsulated spores which split open, and out of each spore emerges a single amoeba. This amoeba immediately begins to feed on the bacteria that are supplied as food, and after about three hours of eating they divide in two. At this rate it does not take long for them to eat all the bacteria on the agar surface – usually about two days. Next comes the magic. After a few hours of starvation, these totally independent cells stream into aggregation centers to form sausage-shaped masses of cells, each of which now acts as an organized multicellular organism. It can crawl towards light, orient in heat gradients, and show an organized unity in various other ways. It looks like a small, translucent slug about a millimeter long (indeed, this migrating mass of amoebae is now commonly called a 'slug'). It has clear front and hind ends, and its body is sheathed in a very delicate coating of slime which it leaves behind as it moves, looking like a microscopic, collapsed sausage casing … After a period of migration whose length depends very much on the conditions of the slug's immediate environment, the slug stops, points up into the air, and slowly transforms itself into a fruiting body consisting of a delicately tapered stalk one or more millimeters high, with a terminal globe of spores at its tip (pp. 3–4).

Like Thoreau, Bonner extracts moral lessons from his close observations of the living world. Noting that the leading cells at the front end of the crawling slug die, while the laggard cells in the hind region turn into spores and are the sole contributors to the next generation, he comments: 'Slime molds seem to support the old army principle of never going out in front – never volunteer for anything.' In a similar vein, after discussing the seasonal variation between sexual and asexual reproduction in the colonial alga *Volvox*, he hypothesizes that the 'strategy is that if you have a good gene combination and the conditions of growth are ideal and constant, then multiply as rapidly as possible without the expense and complication of gene shuffling As soon as there is uncertainty as to the future, hedge your genetic bets for the next season by producing genetically variable offspring'.

Bonner's fascination with *Dictyostelium* and other social microorganisms has caused him to consider the significance of each step along the pathway that leads from the single cell, to the integrated multicellular state, and then back again to the single cell. Hence the importance of the idea of the 'life cycle' as an integrating concept for development and evolution. 'The great lesson that comes from thinking of organisms as life cycles,' Bonner states, 'is that it is the life cycle, not just the adult that evolves.' Those of us who work in the field of animal development are often lulled by the lockstep nature of embryogenesis, with its built-in redundancies, backup mechanisms, and parallel pathways for achieving each developmental end-point, into forgetting that the *evolution* of pattern and form must have occurred in cellular populations whose multicellular embodiments were more directly subject to the formative forces of the external world than are present day embryos. In other words, during the early stages of the evolution of development, the cell types that interacted with each other and their physical environment to generate a particular morphological outcome were the same cell types that gave rise to new organisms. This remains the case for some present-day organisms like *Dictyostelium*, but not for the Weismannian creatures which are the mainstream subjects of developmental and evolutionary biology.

Bonner's own work is replete with examples of insights that arise from his seeking answers where it would have been easy to overlook the fact that something needed explaining. One early problem that he took up was the question of why slime molds, and all other small fungi with fruiting bodies, rise straight up into the air at right angles to the substratum, regardless of the orientation of the substratum. By cutting a migrating slug up into three pieces, and moving them around 'as in the shell game,' he found that he could produce three fruiting bodies, at least two of which leaned away from the vertical. He eventually concluded that there was a repulsion between the rising fruiting bodies, and that it was due to their release of a volatile substance. With the help of Princeton's Department of Aeronautical Engineering he built 'the world's smallest wind tunnel' and tested this idea, producing novel fruiting body configurations, consistent with the hypothesis of a gaseous morphogen. The gas proved to be ammonia, as eventually demonstrated by Bonner and his coworkers. The fruiting body stands up straight under normal circumstances because the repellent it gives off is uniformly distributed.

Bonner is a great admirer of Darwin. Indeed, one of his recent monographs is entitled *The Evolution of Complexity by Means of Natural Selection* (Princeton, 1988), and references to Darwinism abound in the present memoir. However, Bonner's natural integration of developmental processes into his view of life takes him to places where orthodox Darwinians fear to tread. Darwin himself had little appreciation of developmental phenomena, inventing the peculiar 'hypothesis of pangenesis' late in his career to account for the transmission of traits across generational lines. This theory held that each cell type in the body produced, and was represented by, invisible particles called 'gemmules', which circulated freely throughout the system and accumulated in the reproductive organs. New individuals, in part similar to their parents, and in part different, would result from the mixing of these gemmules during fertilization.

Darwin's theory of development thus proposed a radical separation between an organism's material properties and the 'information' required to generate it anew. Rather than being discarded as more sophisticated genetic concepts entered biology, this separation was upheld by Darwin's followers such as Weismann and later adherents of the idea of the 'genetic program'. Richard Dawkins, a prime exemplar of this tradition, puts it characteristically: 'What lies at the heart of every living thing... is information, words, instructions.... If you want to understand life, don't think about vibrant, throbbing gels and oozes, think about information technology.' (*The Blind Watchmaker*, Norton, 1986, p. 112). Bonner's rejection of this sterile view is manifest throughout *Life Cycles*:

[D]evelopment does not consist only of the synthesis of new proteins, but.... many other subsequent processes play a vital role.... During development there are complex networks of chemical reactions that were initiated by the genes and their initial products but will later be largely divorced from the genes which gave birth to them and will carry on an interacting, interlocking life of their own.... These sequences of chemical reactions do not, in themselves, explain the pattern of a developing organism; something more is needed. One answer to the problem came from mathematicians who showed that by the combination of chemical reactions and physical forces, such as diffusion of the molecules and the flowing properties of the liquids, theoretically all sorts of patterns can be produced (pp. 84–85).

Bonner's dynamical picture of development leads him to a heterodox view of the evolutionary process. This is exemplified in his championing of the work of D'Arcy Thompson and J. Mark Baldwin, two biological theorists from earlier in this century whose work had been dismissed or minimized by the architects of the neo-Darwinian synthesis. D'Arcy Thompson, whose writings have remained accessible mainly through Bonner's elegant abridgement of his 1917 and 1942 books *On Growth and Form* (Cambridge, 1966) argued, using numerous examples, that the material properties of cells and tissues, such as surface tension, viscosity, elasticity, and stress–strain relationships, have a profound role in determining why organisms and organs have the structures that they do. In the introduction to his edition of *On Growth and Form* Bonner notes that these ideas, particularly as they relate to evolution, 'were heretic in 1917 and it must be admitted that, for partly different reasons, they remain so today.'

This is the case, as Bonner goes on to discuss, because contemporary biology is so thoroughly committed to the idea that 'the particular gene complement of an organism is directly, through spatially organized chemical reactions, responsible for 'growth and form'. Moreover, each organism's gene complement is considered to have arisen through selection acting on adult forms in confrontation with one another and their environment. If a given structure (for instance, the cantilever-like arrangement of bone trabeculae which adapts adult bones to bear weight efficiently), arises during embryonic development when it is not subject to external influence (e.g. before any significant weight-bearing takes place), it is difficult to imagine, within the neo-Darwinian framework, how D'Arcy Thompson's notion that physical forces are causally involved in the formation of the structure can be correct

In order to rescue D'Arcy Thompson's powerful vision of a predictive science of biological form, Bonner appeals to the ideas of Baldwin, who proposed that under certain circumstances fortuitously appearing hereditary characters would spread through a population if they produced structures or behaviours similar to those elicited by interaction between individual organisms and their environments. The embryologists I. I. Schmalhausen and C. H. Waddington later showed, independently, that such 'genetic assimilation' could occur if there was selection against variability in outcome of developmental pathways which originally depended on particular environments. In a real sense, therefore, acquired traits or behaviours can guide the accumulation of inherited qualities. George Gaylord Simpson, a founding father of the neo-Darwinian synthesis, considered this class of phenomena, which he referred to as the 'Baldwin effect', to be a 'relatively minor outcome of the theory [of evolution by natural selection]' In contrast, Bonner considers the Baldwin effect to be 'an important and very general principle of biological evolution'.

Indeed, it is clear why orthodox Darwinians would want to minimize ideas like those of D'Arcy Thompson and Baldwin, and of the mathematicians like Nicholas Rashevsky and Alan Turing, discussed by Bonner, who took up the question of the physico-chemical bases of morphogenesis. For if it were conceded that 'intrinsic properties of primitive multicellular aggregates made the evolution of certain features of body plans and organ forms virtually inevitable (segmentation, for example), there would be no need to explain these features in terms of superior adaptation resulting from competition between incrementally different organisms. Neo-Darwinism tends to treat biological information, embodied in the genes, as separable from, and dominant over, biological matter. But as we have seen, this is a position from which Bonner explicitly dissociates himself

While the structure of *Life Cycles* follows the evolutionary progression of life on earth, beginning with phenomena that pertain to individual cells and culminating in a chapter dealing with human culture, it also neatly parallels the trajectory of the author's own intellectual development. Bonner has taken up questions at progressively higher levels of integration over the course of his career, producing, in addition to the classic treatise on his chosen experimental system, *The Cellular Slime Molds* (2nd edn., Princeton, 1967), monographs on *Size and Life* (with T. A. McMahon; Scientific American Books, 1983), *The Evolution of Culture in Animals* (Princeton, 1980), and the previously mentioned *Evolution of Complexity*. His forays into fields in which he has not been a primary investigator are made with due circumspection, but unapologetically, and he brings to them fresh insights on the order of those which he brings to his own research. Partly because of the explosive increase in specialization, the twentieth century has lacked great systematizers of biology such as Buffon and Darwin in their respective periods. Of contemporary scientists, John Bonner comes closest to providing a conceptually integrated overview of the main streams of modern biology. Furthermore, his understanding of the complex relationships among gene activities and forms and behaviours in 'simple' systems enables him to steer clear of the genetic reductionism that characterizes much writing by biologists on social and cultural issues.

His discussion of mobbing behaviour in European blackbirds is a particularly good example of his conceptual approach to these subjects. This behaviour is elicited by birds of prey, such as owls or hawks, and draws the attention of other members of the blackbird flock to a potential attacker Bonner describes an experiment by some German investigators in which one blackbird was shown a stuffed honeyeater, a harmless species, while a nearby blackbird was shown a stuffed owl, which sent it into an audible frenzy. The first bird took its cue from the behaviour of the second, and eventually taught still a third bird to mob the honeyeater. The conclusion is that such behaviours can be 'culturally' transmitted after they arise in a single generation. But Bonner notes that birds also have hereditary dispositions which control behaviour so that a particular predator or its silhouette is recognized without any prior learning As with the developmental phenomena discussed above, he invokes the Baldwin effect to account for this interplay between acquired and inherited behavioural propensities 'It would seem reasonable that if an animal behaves the same way (through selection) for numerous generations, genes could seep in by chance to fix those behavioral traits .. If there is selection for a trait, or no selection either for or against a trait that keeps repeating itself in successive life cycles, then there are good chances that genes will appear that ensure the same thing.' Hidebound neo-Darwinists would recoil at the Lamarckian sound of this, but it is perfectly good genetics and perfectly good evolution. Bonner's deep appreciation of the organism-environment dialectic causes him consistently to place *biology* in the lead in his accounts of evolutionary change.

Remarkably, for a book of only 200 pages which spans such a wide range of scientific topics, *Life Cycles* is written in a lucid, seemingly effortless style, and is interwoven with amusing reminiscences from different stages of the author's scientific career Bonner's matrix of friends and acquaintances has been unusually rich, and he takes numerous opportunities to express gratitude to those that have helped him along his way. Like his dispatches from the microbial world, the reports of his encounters with scientific heroes and peers wryly illuminate his subjects Thus we get to hear J. B. S. Haldane, encountering the young Bonner in the 'gents' after he had nervously delivered a lecture at University College, London, chiding him about his American predilection to put jokes in his lectures Having met both Whitehead and Einstein he got to ask them on separate occasions about the one time they had been introduced to each other. The two men's explanations for why they barely exchanged a word speak volumes about their different temperaments.

Like his marvellous but easily overlooked *Dictyostelium*, the originality and importance of Bonner's scientific vision can be veiled to a certain extent by its modest, natural setting. He is, withal, a giant of twentieth century biology, and this gem of a book is as good an introduction as any to the style and content of his thought

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