A Commentary on Blute's 'Updated Definition'

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Barely a decade after the discovery of the chromosomal basis of inheritance, and the articulation of the genetical theory of population change, the gene came to be widely regarded as the fundamental unit of biological organization. This is hardly surprising. The gene concept is a powerful one; it plays a unifying role in our understanding of evolution. Darwin told us that evolution by natural selection occurs in a population when organisms survive, die and reproduce differentially on account of their heritable form (what we now call 'phenotype'). This is a very schematic theory. It requires an account of the process of inheritance and also an account of the generation of phenotype. The gene concept plays a prominent role in explaining, and uniting, these phenomena. Genes are the units of inheritance; they are passed from parents to offspring in reproduction. Moreover, they are seen as units of phenotypic control. Evolutionary biologists often speak of the genome as a program for the production of an organism. Genes also became the elements of which populations are composed. Our best theory of population dynamics—inherited from Fisher, Haldane, and Wright—is a theory of changes in the relative frequencies of gene types. Genes are not just the principal causes of evolutionary change, they are also the units over which evolutionary change is defined and measured. So, at least, the orthodox reading of the Modern Synthesis theory of evolution would have us believe.

The successes of this gene-centred evolutionary biology hardly need recounting. But one may celebrate its successes without succumbing to its excesses. Since the 1980s an alternative movement in evolutionary biology—evolutionary developmental biology ('evo-devo') and ecological-evolutionary-developmental biology ('eco-evo-devo')[1]—has been gaining prominence. Evo-devo seeks to rein in the rhetoric of gene-centred biology, and to offer a more realistically organism-centred perspective on the process of evolution (Callebaut, Muller and Newman 2007). Marion Blute's revised definition of evolution by natural selection is a contribution to this conceptual reconfiguration of evolutionary biology, and a welcome one. Professor Blute proposes that we think of evolution by natural selection in the following way:

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[1] I shall use these terms interchangeably to refer to a single body of thought, although I recognize that each encompasses a variegated assemblage of nuanced views.

> Microevolution by natural selection is any change in the inductive control of development (whether morphological, physiological or behavioral) by ecology and/or in the construction of the latter by the former which alters the relative frequencies of hereditary elements in a population beyond those expected of randomly chosen variants. (Blute 2008, 4)

Professor Blute's definition departs from the received Modern Synthesis account—according to which, evolution by natural selection is change in gene frequencies due to differential fitness—in three significant ways: (i) its use of the concept of '*hereditary elements*' instead of 'genes', (ii) its emphasis on the *construction of ecology by development*, and (iii) its identification of *development as the object of evolutionary change*.

The differences are brought into stark relief by a consideration of the respective roles of the organism in Modern Synthesis and eco-evo-devo biology. It is often remarked that Modern Synthesis biology has issued in the marginalisation of organisms (Hamburger 1980; Dawkins 1983; Gould 1983, 2002). Modern Synthesis biology doesn't deny the existence of organisms, of course, but it accords them very little explanatory role. Organisms are mere middlemen in the Modern Synthesis version of evolution, the interface between the genetic control over the phenotype and the environmental forces of selection. Eco-evo-devo, by contrast, casts organisms as the agents of evolutionary change. On this view, organisms are self-building, self-organizing, self-regulating entities (Fox Keller 2007). They adapt to their circumstances and interact with, and construct, their environments. These distinctive activities of organisms have important consequences for the process of evolution.

Whereas the Modern Synthesis version of Darwinism explains ontogeny and inheritance by appeal to the capacities of genes, eco-evo-devo appeals to the entire organism/environment system. Phenotypes develop through the constructive interaction of organism and environment, not merely through the actions of genes (Gilbert 2001). The unit of phenotypic control, then, is this extended interactive, organism/environment system. This commitment of evo-devo to the role of organisms accounts for the three salient features in Professor Blute's proposed definition of evolution by selection.

Genes and Hereditary Elements

The objective of a theory of inheritance is to explain the intergenerational stability of phenotypes. Any feature of the organism/environment system that secures this stability ought to count as part of the mechanism of inheritance. Environmental factors can be just as important in underwriting the resemblance between parents and offspring as the transmission of genes (Mameli 2005). The conspicuous absence of the g-word in Professor Blute's definition is intentional and apposite: genes are not the only 'hereditary elements'. A 'hereditary element', in her sense, is any intergenerationally stable phenotypic feature, no matter how its stability is secured.

The Construction of Ecology by Development

Darwin's principal insight is that evolution is caused by variation in the respective capacities of organisms to survive and reproduce given their 'conditions of existence'. Typically, 'conditions of existence' is interpreted as 'environment', the intrinsic, self-standing properties of the extra-organismal milieu. But in so far as the environment is important to explaining evolution, it is the environment *as experienced by the organism*. Organisms assert a significant influence over their experienced environments. They construct them, either by effecting some change to the extra-organismal milieu itself (Odling-Smee et al. 2003), or by accommodating, i.e. by effecting some compensatory developmental internal change. If organisms' 'conditions of existence' are explanatorily important for evolution, then organisms' capacity to alter those conditions ought to play a prominent role in evolutionary explanation—hence Professor Blute's emphasis on the construction of ecology by development. The capacity of ontogeny to influence ecology is an important contributor to the process of evolution.

Development as the Object of Evolutionary Change

The feature of organisms that permits them to alter their experienced environments is phenotypic plasticity. Biologists are beginning to recognize the pivotal role of plasticity as a driver of adaptive evolution. One aspect of plasticity, phenotypic accommodation, is particularly significant.

> Phenotypic accommodation is adaptive mutual adjustment, without genetic change, among variable aspects of the phenotype, following a novel or unusual input during development (West-Eberhard 2003, 98).

If one part of an organism's developmental system accommodates to the exigencies of the environment, other compensatory changes that secure the well-functioning of the organism will generally follow. '[A]ccommodation involves the re-use of old pieces in new places' (West-Eberhard 2005, 617), with new functions. It even involves the co-option of old genes into the production of these new, developmentally induced structures (True and Carroll 2002). A change in the relative frequency of those genes that underwrite the reliable production of these novel phenotypes will ensue. Here we see the importance of Professor Blute's emphasis on developmental systems as the objects of adaptive evolution. In the organism-centred model, developmental systems initiate adaptive change. Genes are enlisted to stabilise, or 'routinise' the production and transmission of novel phenotypes. Genetic change certainly does occur in adaptive evolution, but it is the consequence, and not the cause, of the production of adaptive novelty: "genes are followers in evolution not leaders" (West-Eberhard 2003).

The empirical successes of eco-evo-devo over the last fifteen years have radically altered our understanding of the processes that contribute to adaptive evolution. The greatest dividend has been the realization that the capacity of organisms to react adaptively to their internal and external 'conditions of existence' is of cardinal importance. Conceptual change has lagged behind these empirical advances. Evolutionary developmental biologists are growing increasingly concerned to understand how this organism-centred biology should impact on our understanding of the role of natural selection in adaptive evolution (Gerd Müller pers. comm.). In my view, Professor Blute's proposed definition goes a long way toward reconfiguring the concept of natural selection in a way that is appropriate to the new science of eco-evo-devo.

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