

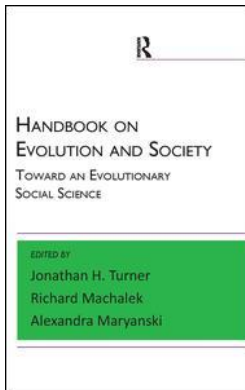
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### **Modes of Variation and Their Implications for an Extended Evolutionary Synthesis**

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### CHAPTER THREE

## MODES OF VARIATION AND THEIR IMPLICATIONS FOR AN EXTENDED EVOLUTIONARY SYNTHESIS

*Marion Blute*

This chapter synthesizes modes or principles of variation in evolution. This is not usually done and is important because it is often assumed that evolutionary theory has little to say about variation beyond the idea that it is “random,” that is, “non-prescient” (Campbell 1956), and hence, among other things, there is nothing to generalize from to a sociocultural context. But there are such principles—at least some. These include basic logical sets of kinds of variations; modularity; major transitions; evo-devo; von Baer’s laws; nongenetic inheritance including culture, origins, and rates of innovation; and forms of introgressive or reticulate evolution (i.e., evolutionary nets). Moreover, most of these modes or principles of variation have implications for subsequent evolution and are currently under active theorizing and research—a large part of the effort under way to achieve an extended evolutionary synthesis.

### BASIC KINDS OF VARIATION

There is a basic set of kinds of variation—mutations (as they are called in biological evolution) or innovations or inventions (as they are commonly called in sociocultural evolution—including here for convenience linguistic, economic, and scientific and technological evolution). These are adding, subtracting, substituting, and rearranging elements. The meaning of adding and subtracting is self-evident, but substituting implies a combination of adding and subtracting, of roughly the same amounts in the same location. The first car I drove had a heater, but since then air conditioning has been added, running boards have been removed, front-wheel drive has replaced rear-wheel drive, and the controls have been extensively rearranged. Moreover, all four of these can take place at a variety of scales in both realms. A biological mutation may involve anything from a single genetic element (in structural terms a base pair, or in functional terms a three-base pair codon) all the way through a whole chromosome or even a whole set of chromosomes. Socioculturally, an innovation may affect a single idea or norm or value—all the way through an entire role or status, organization, or even an entire institution such as a kinship or a religious, political, or economic system (Abrutyn 2014). Developmental biologists as opposed to evolutionary biologists prefer a different classification suggested by phenotypes (observable characteristics) rather than genotypes—heterotopy (change in location), heterochrony (change in time), heterometry (change in amount), and heterotypy (change in kind) (Arthur 2011). In either case, the four basic types or

modes of innovation are simply logically possible categories and, by themselves, have no particular evolutionary implications. What follows utilizes the first classification. The section on modularity and origins is about adding; the section on major transitions is about whether something is substituted or added. Sections on evo-devo, von Baer's laws, nongenetic inheritance, and whether innovation rates are selectable apply to all four kinds of innovations. Finally, the section on evolutionary nets is about whether something is added or subtracted.

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### MODULARITY: PARTS GIVE RISE TO MORE PARTS

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In the 1960s Susumu Ohno (1970) made an important discovery and elaborated an important principle—"evolution by gene duplication." He discovered that additions to genomes come from overduplication of existing genomic sequences. These duplications can range from a single base pair all the way to an entire genome (called polyploidy). His view was that duplication of (usually part of) an existing genome had the effect that the redundant copy was free to gradually evolve to take on some new function, enabling the evolution of complexity. Common descent originating internally in this way is termed "paralogy" or "serial homology" by analogy with the more familiar external "homology." Since Ohno's time, important new observations and ideas have been added. For example, not only can redundant copies of genes take on new functions, but the old and the new can specialize in different aspects of the old function, or the new can take on control functions—genes acting to flexibly control the activities of other genes.

Evolution by endoduplication takes place not only genetically but at a whole host of levels of biological organization—the whole phenomenon coming to be known as "modularity" (for an overview see Raff 1996 and the articles in Callebaut and Rasskin-Gutman 2005). Modules differentiated by function are explicable, the principle being that specialists (in this case specialist parts) are commonly more efficient in what they specialize in than are generalists in that part. But what of unspecialized or repetitive modularity? Insect abdomens typically have eleven or twelve segments, the first seven or so of which are typically undifferentiated from each other. The structure of vascular plants is divided into roots and shoots (the latter composed of stems and leaves), but branches of both give rise to branches that themselves give rise to branches, and so on, yielding a fractal pattern (one that is self-similar on more than one scale). So are such phenomena simply indicative of a principle of variation, of origins by overduplication, or do they also have evolutionary implications in the sense that there is also some general reason why they have been selected? Many think they do and there is. In particular, by functioning semiautonomously, even such undifferentiated modules can enhance overall performance while at the same time minimizing connection costs (Clune, Mouret, and Lipson 2013), ultimately increasing "evolvability" (for a review see Arenas and Cooper 2013).

Socioculturally, enterprises are known to do this as well—employing loosely coupled departments or divisions, creating semiautonomous profit centers (for an overview see Baldwin and Clark 2000). If endoduplication is one of the most important modes of variation by which complexity is increased, major transitions or additions are the other.

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### MAJOR TRANSITIONS: WHOLES GIVE RISE TO MORE WHOLES

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#### MAJOR TRANSITIONS

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With modularity, parts give rise to more parts, but in major transitions, wholes give rise to more wholes. In their book *The Major Transitions in Evolution*, Maynard Smith and

Szathmáry (1995) initiated a significant new stream of theory and research in evolution that continues to this day. “Major transitions” was not meant in the broad sense of key innovations such as the invention of photosynthesis, movement, or warm-bloodedness (Calcott and Sterelny 2011: 4; Lane 2009). Rather, it was meant in a narrower sense that “entities that were capable of independent replication before the transition can replicate only as part of a larger whole after it” (Maynard Smith and Szathmáry 1995: 4). They included a long list of such hypothesized transitions in their survey—“the origin of life, of the genetic code, of cells, of sex, of multicellular organisms, of societies, and of language” (xiii). Later researchers have tended to focus on paradigmatic cases such as the evolution of eukaryotic cells (which include organelles that were once free-living prokaryotic cells), the evolution of multicellularity from unicellularity, and the evolution of eusocial colonies from multicellularity (e.g., Michod 1999 on cells and multicellularity). As Bouchard and Huneman (2013) later put it, in major transitions evolution has gone “from groups to individuals.” While some prefer the term “organisms” (see some of the essays in the former collection) or even “mergers and clubs” (Baptiste et al. 2012), most have continued to talk about the evolution of new kinds of collective or aggregate “individuals.” Godfrey-Smith (2009) described “Darwinian populations” and “Darwinian individuals” and major transitions as “the appearance of new entities that can enter into Darwinian processes in their own right” (122). In many cases (including the eukaryotic cell and multicellularity) this involves “changes to the status of collective entities” in which, as the new collectives gradually become “Darwinized,” the old gradually become “de-Darwinized” (122–128), although he is somewhat ambivalent about the latter, as was Michod (1999) to some degree.<sup>1</sup>

Bourke (2011) argued that such transitions take place in three stages, which he called social group formation, social group maintenance, and social group transformation. For multicellularity, such stages might be described as follows:

1. A metapopulation of evolving cells in a population of multicellular organisms (i.e., before the transition only the cells are evolving)
2. A metapopulation of evolving cells in a population of evolving multicellular organisms (i.e., during the transition both are evolving)
3. A metapopulation of cells in a population of evolving multicellular organisms (i.e., after the transition only the multicellular organisms are evolving). In Godfrey-Smith’s (2013) terms, in the last stage the cells have finally been “de-Darwinized.”

#### MAJOR ADDITIONS

The alternative to this “replacement” view of transitions is that the second stage never disappears; that is, there is always a metapopulation of evolving prokaryotic cells in a population of evolving eukaryotic cells, a metapopulation of evolving cells in a population of evolving multicellular organisms, and a metapopulation of evolving multicellular individuals in a population of evolving eusocial colonies. On this view, evolution on the original level has not been replaced. Instead, it has become “encapsulated” (Blute 1977, 2010: 193) or “nested” (Nachtomý, Shavit, and Smith 2002) as it becomes the mechanism of development of individuals in the newly added evolving population. Such a view was traditionally defended by Buss (1987) and more recently by Kupiec (2009), who emphasized the stochastic nature of gene expression, and by Clarke (2011) for root and shoot meristems in plants.

A hierarchical “fate map” of a multicellular animal such as *C. elegans* is a tree. Unlike familiar evolutionary trees, however, these developmental trees are repeated and

constricted enough in time and space to be experimented on. Stimulated by Weismann's original view of the segregation of determinants in development and eventually the difference of opinion between embryologists Roux and Driesch, generations of classical embryologists did innumerable transplantation experiments on a variety of model animals (but most commonly amphibians) to test whether development was "mosaic" or autonomous (ancestry matters) versus "regulative" or dependent (the local environment matters). If you transplant part of an embryo replacing a part somewhere else, does it become what it would have become in its original location (i.e., ancestry matters), or is it regulated by the new environment to become what would have developed there from what was removed (i.e., the local environment matters)? The answers found varied by group and by the part of the embryo involved. The most general finding was that the earlier the stage of development, the more regulative, while the later the stage, the more mosaic (i.e., heritable changes in cell groups, their lineages, and cells themselves eventually come into existence in development; see any traditional text in developmental biology). Add to this the facts that cell death ("apoptosis") and differences in cell proliferation rates are also parts of normal animal development. Hence, to argue that this is *not* evolution among cells one would have to argue that, even so, the heritable differences as opposed to the nonheritable ones among cells make no difference to what cells survive and proliferate and what ones do not—an argument that would surely be special pleading. So there is variation (called differentiation) in development, inheritance, and differences in fitness—this is evolution by definition. The existence of cancer is only the most obvious manifestation of the fact that the evolution of multicellularity is an addition and not a replacement.

A simple model of a mechanism of transition by addition may make this clear. It has been suggested that the condition necessary for a major transition is a minimum of two alternative strategies, each of which, as a by-product, constructs the ecological conditions that favor the other. Gradually, those conditions come to induce (or the conditions predicting them come to induce) the other strategy such that a new aggregate developmental life cycle (i.e., one capable of repeating itself) emerges (Blute 2010: 191). Assume that in a patchy environment we begin with a metapopulation of cells in a population of many small cell groups (whether originating "fraternally" [i.e., by descendants "staying together"] or by "egalitarian" means [i.e., by the unrelated "coming together"]—see Queller 1997; Tarnita, Taubes, and Nowak 2013). Cells in groups on patches with plentiful resources grow and multiply, while those in groups on patches with scarce resources die off, creating a population of fewer, larger groups. At that point, selection favors groups dividing and dispersing into patches that previously had few resources but now have had an opportunity to recover. This creates a population of more numerous smaller groups again. Why disperse in subgroups rather than as a whole? That is easy—because subgroups can disperse in more directions. But then at the opposite extreme, why not disperse as single cells rather than as cell groups? Surface area increases less than linearly with volume. As a consequence, all other things being equal, groups encounter proportionately less resistance than do single cells in moving. Moreover, while the small (single cells) are better adapted to consume (eat and excrete), the large (cell groups) are better adapted to digest (break down and build up). Hence subgroups are better able than single cells to move and sustain themselves as they move until they arrive where resources are plentiful again.

Such a mechanism can be realized in the simplest case in a haploid asexual population in which two alternative alleles expressed in cells and in groups of them are competing, going respectively from a  $+ -$  relationship to  $- +$  and back again. In Okasha's (2006) terms, causal, cross-level by-products obtain in both directions between "particles" and "collectives," but here changing directions cyclically. In Michod's (1999) terms, covariances

between traits and fitness obtain for both lower- and higher-level entities, but here changing signs cyclically. As cycles repeat, selection will also favor these alleles or genotypes evolving to anticipate the conditions that favor them or even using signals that predict those conditions to behave appropriately. By such means the cell growth and multiplication phase becomes the somatic growth phase, and the cell group division phase becomes the reproductive phase (between which there is a trade-off in the allocation of resources) of the new, additional, multicellular kinds of individuals reproducing by multicellular propagules.<sup>2</sup> This simple case is a semelparous life cycle (big bang reproduction all at the end of the life cycle). Possibilities other than switches between growth and motility/maintenance in a patchy environment include the same in a colonizable environment (on the general importance of the latter see Waters, Ceridvven, and Hewitt 2013) or between growth and mutability in one patchy in niche (there is likely to be sampling error and therefore novelty introduced when fewer large groups divide).

### *SOME COMPARISONS*

Okasha (2006) emphasized that Maynard Smith and Szathmáry turned the old problem of units of selection into a dynamical historical one about the evolutionary emergence of new ones. But understanding transitions as innovations, not by replacement but by addition, particularly with the kind of model described above, makes them dynamical in a second sense as well—a developmental one; together they compose an *evo-devo* dynamic. While providing a fundamental theoretical rationale for the existence of multiple levels of selection at all, they also limit the latter. Where an addition by such a means has taken place and a new aggregate life cycle has emerged, multiple levels of selection exist; but where it has not, they do not.

Multiple levels of selection characterize the sociocultural world as much as they do the biological—the world of information or ideas manifested in behavior and artifacts (Mesoudi, Whiten, and Laland 2004, 2006), norms and values governing a variety of these depending on circumstances, social roles or status, organizations, institutions, and even whole cultures and societies. Moreover, a developmental process characterizes at least some sociocultural entities as much as it does the biological. “No act or artifact is an instantaneous event but grows and develops over however shorter or longer a period of time. Whether it is a task being carried out, a sentence uttered, a social role maturing, a hand axe being napped, or a car being built on an assembly line—all have a shorter or longer period of somatic growth and development” (Blute 2013: 111). However, an additions view of transitions with evolution among the old becoming the mechanism of development of the new does place limits on how far these extend. Certainly culturally transmitted ideas, behaviors, and social roles have a life cycle that is reproduced. However, for most organizations, let alone institutions such as kinship and religious, political, or economic institutions consisting of multiple roles and even organizations, let alone whole cultures and societies, that life cycle is at best singular (i.e., evolution among them is only viability rather than reproductively based). Hence, they constitute units of selection only in that very limited sense.

An “additions” as opposed to a “replacement” view of major transitions should not be taken to mean that there are no differences between evolution on lower and higher levels—among cells as the developmental mechanism of multicellular individuals, for example, and conventional evolution. Despite the fact that multicellular organisms including humans are increasingly being shown to be genetic mosaics (for an overview see Lupski 2013), it is likely that most of the heritable differences in cell groups, their lineages, and cells themselves in multicellular development are epigenetic rather than

genetic. Even so, it can be experimentally shown that competition among cells takes place (e.g., Claveria et al. 2013). It also seems likely that much of the heritable change of whatever type comes to be internally “directed” in development in a way that it is not in evolution. Overall, a somewhat analogous case is the relationship between individual learning and social learning and sociocultural evolution. While we can consider the two selection processes separately (whether viewed as analogous or as two tokens of the same general type, selection processes), it is unlikely that one would want to argue that individual learning ceases once social learning and cultural evolution have been added. To extend a metaphor that has been used, an additions point of view is neither “deflationary,” recognizing evolution on the lower level only, nor “inflationary,” recognizing it on the higher level only, but both simultaneously.

As emphasized in the titles of this and the previous section, in the introduction of a new module, parts give rise to more parts, while in a major transition, wholes give rise to more wholes. However, they are similar in that they are probably the two most interesting modes of variation in evolution because they are the most important means by which complexity is added. It is not that increases in complexity are inevitable or even usual in evolution. Most prokaryotes have remained prokaryotes, most unicells have remained unicells, and most multicellular individuals are not part of eusocial colonies, for example. Similarly, most lineages have not become clans, most clans tribes, most tribes nations, or most nations empires. So while such increases in complexity have not in fact tended to prevail in evolution, we still seem to find them the most interesting. Why that is so is puzzling, but it does perhaps suggest that the pre-Darwinian concept of evolution rooted in the medieval “great chain of being” (Lovejoy 1936) still echoes down through the ages. Even Bourke’s use of the term “stages” rather than “states” for evolutionary transitions, like that of traditional “evolutionary” social science (for a history see Sanderson 2007), carries an echo of this as if movement through such a sequence in phylogeny is inevitable in the same way that movement through such a sequence in ontogeny is more or less once established.

### EVO-DEVO: GENES AS FOLLOWERS AS WELL AS LEADERS?

Dobzhansky famously defined evolution as the “gradual change of gene frequencies within populations” that “serves, by extension, as an adequate model for all evolutionary events” (1937: xxiv). But the “by extension” simply glosses over too much. In particular, as has often been pointed out, the definition recognizes the role of heredity in evolution but ignores those of development and of ecology.

Consider two of the ways in which evolutionary innovations can be initiated (both simultaneously are conceivable, but far less likely). In the one “inductive-type”<sup>3</sup> pathway of old genes or gene combinations in a new environment, phenotypes lead and genes follow. If a new food source becomes available that the carrier of some preexisting genetic alternative but not others is able to make use of, the former is ecologically induced by the new diet to grow more, live longer, or have more or better offspring, ultimately resulting in an evolutionary-genetical change in allele frequencies in the population. This has long been known as a pre-adaptation or exaptation (Gould and Vrba 1982). In the other “constructive-type” pathway of new genes or gene combinations in an old environment, genes lead and phenotypes follow. If a new genetic mutation or recombination enables its carrier but not others to “construct” (Odling-Smee, Laland, and Feldman 1996) its ecological niche differently, to use a preexisting but unutilized resource, for example, the carrier’s development is altered similarly, resulting in an evolutionary-genetical change.

To recognize the role of development and ecology in evolution and to include exaptations by formally acknowledging the existence of both of these pathways (as well as other things—microevolution does not in itself incorporate a theory of speciation, and there can be nongenetic as well as genetic inheritance), taking a lead from Van Valen's definition "evolution is the control of development by ecology" (1973), the following definition has been suggested:

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 (genetic or other) hereditary elements in a population beyond those expected of randomly chosen variants. (Blute 2008: 4, 2010: 168)

Ingeniously, Schwander and Leimar (2011: 149) used ancestral state reconstruction methods to determine how commonly switches and losses have taken place between genetic polymorphisms and polyphenisms and found "no clear tendency for genes to be followers or leaders overall," which underlines the importance of a more inclusive definition. In short, recognizing that genes are as likely to be followers as leaders in evolution by employing a more inclusive definition of evolution by natural selection is long overdue.

Such a recognition fits within the definition of the subject matter of evolutionary developmental biology (evo-devo) by the author of its first textbook, Brian K. Hall, who defined it as "how development (proximate causation) impinges on evolution (ultimate causation) to effect evolutionary change and how development itself has evolved" (1992: 2). It might not satisfy those content with the traditional definition or even those to whom evo-devo is primarily the comparative molecular genetics of development—particularly of "tool kit" genes, which regulate the level, location, or timing of the expression of other genes (e.g., see Carroll 2005). At the opposite extreme, it might also not satisfy more radical revisionists who would see interaction between environments and phenotypes as necessarily adaptive, that is, who would revert to a pre-Darwinian teleology (readers can decide for themselves how far in that direction works such as those of West-Eberhard 2003, Jablonka and Lamb 2005, and some of the essays in Sansom and Brandon 2007, Gissis and Jablonka 2011, and Hallgrímsson and Hall 2011 go). While phenotypes can be plastic to be sure, can evolve to bet hedge under uncertainty, or can be adaptively plastic under uncertainty with reliable cues (Roff 2002), *novel* environmental influences on phenotypes are more likely to have maladaptive than adaptive effects, just as novel genes do. Robertson, Rehage, and Sih (2013) well reviewed the former fact under the rubric of "evolutionary traps." The fact that inductive-type innovations are similar to constructive-type ones in that sense does not in any way diminish their evolutionary importance.

The same two modes of innovation should be possible in sociocultural as well as biological evolution—an inductive-type pathway in which a new environment induces an old idea to be manifested in behavior or artifacts differently and a constructive-type pathway involving a new idea in an old environment, with selection then in either case resulting in a statistical change in the composition of a population of ideas. Of course, just as with the biological, there is no evidence that sociocultural innovations are biased *statistically* in the direction required for them to spread successfully. This holds most famously for stock picking and market timing but also for any field one chooses to look at—papers being cited, patents utilized, new businesses succeeding, or new products being successfully marketed (Blute 1979).



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 VON BAER'S LAWS: VARIATION BIASED TOWARD LATER DEVELOPMENTAL STAGES?
 

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In the nineteenth century the great German embryologist Karl Ernst von Baer proposed laws of embryological development—general characteristics and structural relations develop before special ones; the form of an embryo does not converge on that of others but diverges from them; and the embryo of an animal never resembles the adult of another animal but only its embryo. In modern language, embryological development is a process of differentiation in the sense that parts of an embryo become differentiated from each other and that members of different but related groups become more different from each other. Although von Baer was not an evolutionist, Darwin thought that the early similarity of members of different groups was the best evidence for his theory of common descent. As he wrote in the *Origin*, “Community in embryonic structure reveals community of descent” (Darwin [1859] 1958: 417).

Is this pattern of change in development—less change earlier, more later—a principle of variation? Does it mean, for example, that variations in the form of mutations that affect development are more likely to occur later rather than earlier? The consensus view is no, rather than biased mutation, the pattern is most readily explained by constraints. A genetic mutation or recombination that affected the earliest stage of development would have more side effects down the road than would one that first acted later, and many of these would likely be maladaptive. So it is not so much that innovations affecting the later stage occur preferentially as it is that those affecting the earlier stage are selected out preferentially. Analogous phenomena are found in other selection processes. For example, a rat learning a maze with a series of choice points reinforced at the end eliminates mistakes in a backward direction (i.e., change takes place more readily in the later than in the earlier stages of the entire sequence). Undoubtedly it obtains socioculturally as well—in the plans for assembling a new model of car beginning with those for the previous model, for example. The philosopher of biology, William C. Wimsatt, called the constraint principle in the evolution of development “generative entrenchment” (Wimsatt and Schank 1988).

In the 1990s, however, it turned out that the empirical generalization “more evolutionary change has taken place later than earlier in development” does not quite hold—rather, the difference between members of different but related groups resembles an hourglass or an egg timer (e.g., Duboule 1994). Groups differ more in the very earliest phase of development, converge to become more similar (the hourglass narrows to what is called the phylotypic stage, or in animals, the zootype; for a historic overview see Slack 2003), and then diverge again quite a bit for the bulk of the rest of development. Kalinka et al. (2010) confirmed this hourglass pattern for gene transcription involved in key developmental processes by comparing six species of *Drosophila*.

The constraints logic might be taken to imply that the in-between phylotypic stage of minimal change/differences between groups, rather than reduced selection pressures there which has been widely suggested, might represent the actual historical origin of the taxa involved (Blute 2010: 146–148). This interpretation was borne out by Domazet-Lošo and Tautz (2010). Using “phylostratigraphic” methods they had previously pioneered, they found from the transcriptome (all RNA molecules present) that the genes expressed in zebra fish in the equivalent of the animal phylotypic stage are indeed older than those in any other, including the earliest phase. They also confirmed this for some other groups using data from the literature.

But another question remains. Again, if the constraints logic is valid, how has so much evolutionary change in the earliest phase of development been possible? I have argued that it is because what appears to be the earliest phase of development is, in actuality, a

later phase. Such would be the case if it were largely a maternal effect (i.e., a later phase of the mother's development). Intriguingly Domazet-Lošo and Tautz (2010) did find significant differences between the age of genes expressed in the late juvenile and adult phases of males and females in zebra fish with more new genes in females than in males. They suggested this may be related to recent sexual selection (although it should be noted that zebra fish are not notably sexually dimorphic and that there is little evidence that female choice is more significant than male-male competition among them—if anything, the reverse may be the case). However, the sex difference is not really a test of the maternal effect hypothesis anyway. While maternally inherited RNAs would show up in the transcriptome, what would not necessarily show up would be if they were maternally inherited, or transcribed from maternally imprinted genes, or expressed as a consequence of maternally inherited protein transcription factors, for example. Hence, I eagerly await whether the maternal effects hypothesis of “too much” change early in development can and will be tested. If confirmed, von Baer's law would in a sense be restored. I doubt, however, that there is a basis for such “maternal effects” psychologically or socioculturally, although that remains to be seen.

### NONGENETIC INHERITANCE AND CULTURAL EVOLUTION: LAMARCKIAN?

We now know that in a wide range of cases, environmentally induced phenotypic changes can indeed be inherited by a variety of mechanisms, so that is another means by which variation is introduced into a population. The many known examples of nongenetic inheritance have variously been classified into epigenetic, behavioral, and symbolic by Jablonka and Lamb (2005) and into epigenetic, parental effects, ecological, and cultural inheritance by Danchin et al. (2011). One example I like to use is a simple one. Imagine a parental cell that doubles in size and divides once. Then the material included in the two offspring cells (including one strand of each DNA molecule for that matter) was *acquired* by the parental cell rather than *inherited* by it, that is, in this simplest of all cases, the inheritance of acquired characteristics is 50 percent (Blute 2010: 205). We now know that vast genomic hierarchies and networks exist—genes that control the expression of other genes that control the expression of other genes, and so on, at every stage from transcription to post-translation (for an overview see Gilbert 2014, Chapter 2). And the more complex and differentiated the biochemistry is in this way, the more potential targets there are for environmental influences on development as well as for the effects of these influences to be inherited nongenetically. Because a lot more than DNA (which constitutes a very small proportion of a cell by dry weight) is inherited, critics are surely wrong when they make claims such as “the level of the gene is where the conceptual buck stops. More precisely, it is at the level of the genes that the *first* effect of a system that can organize environmental inputs and respond to them, by building more complex systems, begins” (Dickins and Rahman 2012: 2917; italics added).

Critics, however, complain, among other things, that those who emphasize such “Lamarckian” phenomena have not produced a new general theory of heredity, let alone of evolution, to rival Mendel's theory of heredity and the population genetics-based theory of the traditional synthetic theory of evolution (e.g., Dickins and Rahman 2012: 2917). But to be fair, they have generally not claimed to. Rather, Danchin et al. (2011) have called for the development of an “inclusive” theory of inheritance, Jablonka and Lamb (2005) for an evolutionary theory that “acknowledges Darwinian, Lamarckian and saltational processes” (quoted in Dickins and Rahman 2012: 2913), and Pigliucci and Müller (2010) for an “extended” evolutionary synthesis.

On the other hand, it is certainly important to distinguish between Lamarckian inheritance and Lamarckian evolution because the latter carries a lot of baggage in addition to the former. Lamarck thought that there was an inherent tendency to perfection that, as Lovejoy (1936) described it, would drive organisms up the medieval great chain of being. The need to adapt to the environment pushes some off that path, creating a tree. Trees grow taller, giraffes stretch their necks to reach food, and those lengthened necks are inherited by their offspring, he thought. However, it is important to distinguish between inductive environmental influences on phenotypes that organisms have evolved to “expect” (as described in the section on major additions, for example), subsequently inherited nongenetically or not, and those that are novel. Again, novel environmental influences are as (and probably more) likely to induce subsequently nongenetically inherited maladaptations as adaptations. They are no different than subsequently inherited genetic mutations or recombinations in that respect.

It is sometimes thought that this is different when the environmental influences are those controlling learning or involving cultural transmission. It is certainly the case that biological evolution can and often does program the behavior of organisms to be reinforced by, and therefore to learn individually, things that are biologically adaptive—witness the commonness of the reinforcing effects of acquiring food or opportunities for sexual activity in many species. However, because chance is as common psychologically as it is biologically, not all individual learning is biologically adaptive as demonstrated by Skinner’s (1948) famous “superstition” experiments, for example. Moreover, organisms can be programmed to learn by culture as well as by genes. Mesoudi et al. (2013: 189) are certainly correct in claiming that the presence of culture “can create new genetic equilibria that would not exist in the absence of non-genetic inheritance” (e.g., see Boyd and Richerson 1985; Durham 1991; Richerson and Boyd 2005). With cultural transmission and gene-culture coevolution, the direction of inheritance is critically important for understanding its likely biological effects. With vertical cultural transmission (parents to offspring or closely related kin), the relationship between genes and culture is likely to be mutualistic (+ +), not only because genetic evolution will favor the cultural transmission of biologically adaptive traits, but also because cultural evolution will favor the genetic transmission of culturally adaptive traits. With horizontal transmission the relationship is apt to be selfish (+ –), most obviously when sects, cults, and churches appeal to pseudo-kinship to spread themselves at the expense of recruits’ genes, for example. With oblique transmission it is likely to be competitive (– –)—if your biological offspring were to become my cultural offspring and vice versa, then genes and culture would be in competition with each other (Blute 2006a). In conclusion, Lamarckian inheritance, while important, should not be equated with (necessarily biologically adaptive) Lamarckian evolution.

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#### ORIGINS: SINGULAR OR PLURAL? INNOVATION RATES SELECTABLE?

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The ultimate variations, of course, are origins themselves—whether of life, that is, of the biological from the physio-chemical, the psychological from the biological, or the socio-cultural from the psychological—which unfortunately remain among the most poorly understood evolutionary innovations of all. The traditional issue with respect to the origin of life is which one or which combination came first—compartments (membranes), metabolism (protein enzymes), replication (nucleic acid, specifically RNA), or autocatalytic and therefore replicating cycles of protein or RNA enzymes (for an overview see Maynard Smith and Szathmáry 1995). Another approach can be taken from an evo-devo

perspective. If life began as small, simple “juveniles,” then it would seem that development came first and evolution must have developed, but if it began as large, complex “adults,” then it would seem that evolution came first and development must have evolved. While the “small and simple” starting point would seem most logical, if origins were multiple, then viability selection and hence evolution in the form of “competitive development” would have obtained as well (Blute 2006b) with reproduction and ultimately heredity somehow emerging subsequently (e.g., Blute 2007; Salazar-Ciudad 2013). While the near universality of the genetic code might be taken to imply a single origin of life, it actually does not imply that, but only that all forms of life today are descendants of only one of those origins. That is the typical situation in evolutionary processes. As Cavalli-Sforza (2000: 79) made clear, because there was a Y chromosomal-Adam or a mitochondrial-Eve in the human species, for example, does not mean that only one male or one female lived at the appropriate times in Africa. Similarly, even if it were true that all human language families (as opposed to the languages within each family) share a common ancestry, that would not imply that only one group of humans began to talk, but rather that extant language families are the descendants of only one of those that did. So while origins are typically plural rather than singular, descent from one or a small number of these can still be, and often is, the norm.

A related issue is whether *rates* of variation in existing lineages are themselves selectable, a phenomenon sometimes called “adaptive mutation.” The weight of opinion is that they are (Freeman and Herron 2004: 117–118). Mutation rates are thought to be selected for under conditions of stress, a fact particularly well documented in prokaryotes (for an empirical overview and formal proofs see Ram and Hadany 2012). Socioculturally, it is not surprising that since the onset of the recent recession stimulated by the financial crisis, governments everywhere have been seeking more means of increasing scientific, technological, and economic innovation rates and that the Global Innovation Index (sponsored by Cornell University, Insead, and the World Intellectual Property Organization [a UN agency], ranking 142 economies on 84 indicators; see <http://www.globalinnovationindex.org/content.aspx?page=GII-Home>) is being given more attention than it might command in better times.

#### INTROGRESSIVE, ANASTOMIZING, RETICULATE, OR COMPOSITIONAL EVOLUTION: NETS RATHER THAN TREES?

In a letter to J. D. Hooker in 1858, Darwin ([1859] 1958) called his “Principle of Divergence” the “key-stone” of his book, and he also discussed this in the latter part of Chapter 4 of the *Origin*. As Kohn (2009) has made beautifully clear, that was because it linked the other two great principles of his theory, natural selection and common descent (see also Sober 2011: 32–36). Under Malthusian population pressure and ecological interactions, it was natural selection *for* divergence—because that way “*the greatest amount of life can be supported*”—which, along with extinction, gives rise to the branching tree of the history of life (Darwin [1859] 1958: 113, italics added). Moreover, contexts make clear that he viewed this principle of divergence as applying at all levels—among individuals no less than among varieties, species, genera, orders, and so forth (although he sometimes used the term “variety” both for what we would call individual variation and for varieties—the contemporary term “variant” not being in use at the time). In his famous diagram and discussion of it, Darwin showed divergence emerging among individuals within a variety and from that the (two) most distinct varieties and eventually species emerging:

Let (A) be a common, widely-diffused and varying species. . . . Only those variations which are in some way profitable will be preserved or naturally selected. And here the importance of the principle of benefit being derived from divergence of character comes in; for this will generally lead to the most different or divergent variations (represented by the outer dotted lines) being preserved and accumulated by natural selection. When a dotted line reaches one of the horizontal lines, and is there marked by a small numbered letter, a sufficient amount of variation is supposed to have been accumulated to form it into a fairly well-marked variety, such as would be thought worthy of record in a systematic work. ([1859] 1958: 116)

In short, in modern terms, Darwin thought that because it supports more life, disruptive natural selection has thus been responsible for creating the tree of life. However, since all of half a niche is not necessarily better than half of all a niche, that way of “supporting more life” in fact requires a specific condition—namely, that *specialists be commonly more efficient in the range of a niche that they specialize in than are generalists in that range*. And why might that be? It would have to be because they possess some comparative advantage as the economists call it in what they specialize in. Note that all other things being equal, two kinds of specialists would have to be slightly more than twice as efficient, three kinds slightly more than three times as efficient, and so on, which becomes increasingly less likely as the numbers rise. That shows the wisdom of Darwin’s diagram in that while he shows diversity among individuals, in each case he shows only the two most distinct varieties eventually branching off from them, two species from them, and so on—in anticipation of the cladistic understanding that evolution normally takes place by bivariate branching. But his “principle of divergence” explains a lot more than the emphasis on bivariate branching about Darwin’s thinking. That emphasis on the relentless pressure toward divergent specialization explains why he thought species had no more special status than the members of other levels in the taxonomic hierarchy; why he emphasized what we call homology (tree thinking) over homoplasy (parallel and convergent evolution); why he emphasized speciation by ecological rather than by geographic or sexual selection means; and of particular interest here, why he emphasized branching over introgressive, anastomizing, reticulate, or compositional evolution (e.g., Watson 2006).

However, we now know that anastomizing as well as branching processes do indeed take place in evolution—ones including horizontal gene transfer, hybridization, and symbiosis, which, if they prevailed, would make evolution more netlike than treelike. We know that horizontal gene transfer is more common than was once thought, particularly early in the history of life, and still today in prokaryotes, viruses, and other mobile genetic elements. In a few, very rare cases, even cells of multicellular organisms can be horizontally transmitted, like the famous Tasmanian devil facial tumor disease. We know that quite a few plant species are hybrids. We know that the most spectacular example of symbiosis claimed by Margulis (1971; Margulis and Sagan 2003)—that of mitochondria in animals and plastids and mitochondria in plants—is indeed the case. Similar phenomena occur socioculturally. In science, for example, facts, theories, or methods from one discipline are sometimes applied to a problem in another (analogous to horizontal gene transfer); whole disciplines or segments of them sometimes merge, creating a new discipline (analogous to hybridization); and teams of individuals from different disciplines can work together on a problem (analogous to symbiosis) (Blute and Armstrong 2011: 408).

On the other hand, how common horizontal gene transfer is in eukaryotes remains in doubt, and cancers transmissible clonally rather than by viruses are extremely rare; animal hybrids, when formed at all, tend to be sterile; and the other spectacular example

of symbiosis proposed by Williamson (1992, 2003)—that of larval stages in life histories—has been pretty much discredited. As a consequence, most biological evolutionists (but not all—see, for example, Baptiste et al. 2012) still think of the tree rather than the net of life, albeit perhaps a tree with some “cobwebs” (source of this metaphor unknown to me). In the social sciences, I recall at the Cold Spring Harbor Centennial Symposium organized by James Watson in 1990 on “Evolution: From Molecules to Culture,” some of the world’s most prominent historical linguists literally pounding the table at the naivete of some biologists who thought that perhaps languages sometimes merge. Pigeons and creoles notwithstanding, it has never happened, the linguists assured us. That is because a language (as opposed to a dialect) in linguistics corresponds to a species (as opposed to a variety) in biology by definition—that within which individuals are able to exchange communications/genes respectively but not outside of it.

Applications of “tree-thinking” (Baum and Smith 2013), phylogenetic methods borrowed from biology, have become very well developed in the last couple of decades in some social science disciplines, including linguistics, archaeology, cultural anthropology, and even, albeit rarely, for political organization (e.g., Currie et al. 2010), but unfortunately not so far in sociology or economics (for an overview see Blute 2010, Chapter 2; for some recent examples see Buckley 2012, Walker et al. 2012, and Altschuler et al. 2013). Variants of these methods can moreover be used to detect anastomizing processes where they do exist—see, for example, the treatment by Tehrani (2013) of the East Asian “tiger grandmother” folk tale as a probable hybrid of “little red riding hood” and “the wolf and the kids” tales, the latter popular throughout Europe and the Middle East. However, on this issue I think we should give the last word (for now) to David Hull, probably the most prominent philosopher of biology at the time of his death in 2010. In an interview conducted the year before, he said on this point:

Splitting is difficult; merger is even more difficult. The question is why. Splitting is not as common as we thought it was, merger turns out to be more common than we thought it was . . . Now how different and how common is merger in all these areas whether it’s biology or science studies? We have to do empirical research because there’s no a priori answer to that question. (quoted in Blute and Armstrong 2011: 419)

### CONCLUSION: TOWARD AN EXTENDED EVOLUTIONARY SYNTHESIS

Population genetics, uniting Darwin’s theory of evolution with Mendel’s theory of heredity forged in the 1920s and ’30s primarily by Ronald Fisher, J.B.S. Haldane, and Sewall Wright, which banished the Lamarckianism, orthogenesis, and saltationism that had created such confusion in the immediate post-Darwinian period, was a major intellectual achievement. So too was its application in a variety of fields in the synthetic theory of evolution by Dobzhansky, Mayr, Huxley, Simpson, Stebbins, and Rensch in subsequent decades and since. However, evolutionary theory is not static; it continues and will continue to change. Concepts and theories in science vary, are transmitted, and evolve (Toulmin 1972; Hull 1988; Blute and Armstrong 2011). Because of the variety and importance of new ideas and results, there have been calls in recent years for a “new” synthesis or at least for an “extended” one (e.g., Pigliucci 2009 and the articles in Pigliucci and Müller 2010). Not surprisingly, however, there are differences of opinion about what is most important to be included and few claims about what this new or extended theory will look like overall, if indeed it is achieved. I have chosen here to focus on the theme of modes of variation beyond logically basic sets—including modularity, major transitions,

evo-devo, the distribution of variations across the life cycle, nongenetic inheritance including culture, origins and rates of innovation, and compositional or reticulate variation as well as their evolutionary implications.

The call has perhaps been strongest for the need to more explicitly address development in an “evo-devo” theory. Toward that end, and as potential contributions to an extended synthesis, I have emphasized an additions rather than a replacement theory of transitions, a revised definition of evolution by natural selection that incorporates development and ecology, and a historical origins and maternal effects theory of the developmental hourglass. In all of these cases, however, it remains that Darwin was essentially correct. Adaptation is achieved in both the biological and sociocultural realms, not because it is what is sought, but because selection controls what evolves.

## NOTES

1. In his later essay, Godfrey-Smith (2013) seems to be somewhat ambivalent about whether the new kind of Darwinian individuals are added to or replace the old. “As one Darwinian population evolves, it can give rise to new kinds of Darwinian individuals,” which sounds like an addition (i.e., both are evolving). But then he adds, “Darwinian individuals can also go out of focus—lose their Darwinian characteristics,” which sounds like a replacement (i.e., only the new are evolving) or perhaps it is suggesting that some cases are additions and others are replacements. But then he seems to settle on the view that all cases are partly one and partly the other, “The evolution of new individuals *partly* ‘de-Darwinizes’ the old ones that make them up” (24–25; italics added). Finally, the “partly” is modified even further by “tend to”: “collectives *tend to partly* de-Darwinize their constituent parts” (26; italics added). Similarly, Michod (1999) tells us that, on the one hand, in a transition lower-level units go from being selfish to being cooperative, but also that “the tension between lower and higher level units is never completely resolved in any evolutionary transition” so units are “nested but partially decoupled” (4).
2. Later, at least in the case originating by “staying together,” distinct germ line cells could emerge, perhaps by Bourke’s (2011) “virtual dominant” mechanism. Nascent germ cells might emerge from those cell lineages with a lower division and hence a lower mutation rate so that nascent somatic cells would be more related to the former than to each other and hence the former could come to “virtually dominate” the latter.
3. “Induction” has been the traditional term used in embryology for processes in which a part of an embryo causes another part to develop in a particular direction by contact or local diffusion and has sometimes been extended to the influence of the external environment on development. Recently a group of mainly philosophers adopted a metaphor of “scaffolding” to incorporate environmental influences on development, whether biological or sociocultural, and possibly much else as well. The scaffolding metaphor originated in cognitive psychology with respect to learning to build three-dimensional structures (Wood, Bruner, and Ross 1976) and language learning (Ninio and Bruner 1978), both in children, and eventually spread more widely in the educational literature to refer to various ways of supporting the learning of students. At least to some extent, this adoption was attractive to educators because it avoided (rather than solved) debates over behavioral versus cognitive theories of learning, of classical versus operant learning processes, of individual versus social learning, and of social learning by observation versus by verbal instruction. Unfortunately, a full set of statements of this usage with respect to development understood broadly, which is in Caporael, Griesemer, and Wimsatt (2014), was not yet available at the time of this writing. Hence, I have, for now at least, retained the more traditional concept of induction.

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