Changing Conceptions of Evolutionary Theory

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Evolutionary theory has been undergoing a healthy period of ferment for the last two decades. In particular, the view, central to the synthetic theory of evolution, that natural selection acting on small mutations constitutes much of evolutionary change has been severely challenged. New metaphors and mechanisms of evolutionary processes are being developed and debated. These advances, however, have had little impact on the practice of biological anthropology. In part, this is because alternative views are being formulated by specialists outside anthropology while studying other organisms. However, the primary reason why new ideas are slow to filter into the study of human evolution is that the notion of adaptation through natural selection is so ingrained that its status as the only explanatory framework is rarely questioned. This chapter outlines selected areas of recent conceptual development, including a multi-leveled view of causality, developmental constraint, phylogenetic systematics, and the role of behaviour in evolution. The significance of these ideas for interpretation of human evolution and diversity are discussed.

INTRODUCTION

Among scientists today, the idea that humans evolved from an ape-like ancestor several million years ago is no longer controversial. However, just why and how humans evolve, and why there is so much behavioural and biological diversity within the human species, are still
labeledly matters of debate. In other words, while we accept human evolution as an established fact, its mechanisms and causes in both the recent and deep past are far from clear. The lack of consensus amongst anthropologists regarding the mechanisms of evolutionary change reflects the broader intellectual framework within which theories of human evolution are situated. Uncertainty about the mechanisms of evolutionary change is not unique to anthropology, but is indicative of the state of the entire field of evolutionary biology.

Despite the uncertainty regarding the mechanisms or physical causes of evolutionary change, biological anthropologists are united by a commitment to the belief that the diversity, as well as the unity of humankind, is the result of the evolutionary process. The geneticist Dobzhansky’s (1973) aphorism: “nothing in biology makes sense except in the light of evolution” has served as a motto for anthropologists since the formalization in the 1940s of the Neo-Darwinian synthetic theory of evolution, commonly known as the “Modern Synthesis”. Indeed, it is from this view of evolution, with its emphasis on natural selection acting on random mutations as the primary mechanism of change, that most recent anthropological ideas concerning human diversity and evolution arose. The “New Physical Anthropology” advocated by Sherwood Washburn in the late 1950s and early 60s was certainly a direct effort to forge an intellectual link between the Modern Synthesis and the practice of biological anthropology. Not surprisingly, therefore, the anthropological literature on human biology is dominated by selectionist explanations of everything from variations in blood groups, protein and enzyme diversity, and disease patterns, to the enlargement of the human brain, the emergence of bipedalism, differences in skin colour and even the shapes of nose and eyes.

For many years the synthetic view of evolution was virtually unchallenged in North America, but recently it has been questioned by biologists from various disciplines. Evolutionary biology is now besieged by exciting efforts to redirect thinking about the processes of evolution. Curiously, these recent developments have had little impact on biological anthropology and on the conceptualization of human evolution and diversity. This lack of recognition has prompted Colin Groves (1989:vii) to write in the preface to his recent book:

The ferment that has been going on in evolutionary theory for some fifteen years has largely bypassed the anthropological community. Textbooks on human evolution still present

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Natural Selection, acting on Mutation, as The Way in which evolution works; anagenesis, the story of human evolution. [sic] Punctuated Equilibria may get a paragraph; but neutral evolution, macromutations, speciation theory, internal processes, and so on, seem generally not to rate even a mention in most works on human evolution. There are, of course, honourable exceptions, but they are few, often timid, always restricted in scope.

A reading of the recent texts on human evolution and biological anthropology (e.g., Harrison et al., 1988; Klein, 1989; Poirier et al., 1990; Relethford, 1990; Campbell, 1992) certainly attests to Groves’ observation. The primary intent of this paper is to convey the growing realization that evolutionary theory is not solely concerned with the search for optimal or best possible mechanisms of adaptation to the physical environment, but is a research program that contains a plurality of views, beliefs and concepts about organic diversity and uniformity. I will highlight what I perceive to be significant developments in evolutionary biology within the last two decades, and consider their possible impact on the present view of human evolution. This paper is not meant to be an exhaustive review of the literature of evolutionary theory; rather, it is a sampling of the literature that reflects the breadth of the research currently being done on the topic, along with discussion of a number of seminal works that describe the essential concepts that are being developed.

I begin by giving an outline of the central tenets of the synthetic theory of evolution, followed by a discussion of the major sources of the present discontent with this orthodox view. I then introduce several ideas that are emerging out of the recent challenge to Neo-Darwinism in the context of a number of recurring and interrelated themes. These themes have the common thrust of questioning the all-pervasiveness of natural selection and adaptation, and replacing them with a plurality of concepts and reasons for how biological structure and behaviour evolve. The themes, briefly outlined and then discussed in greater detail in subsequent sections, are that:

1. Causality in evolution operates at a number of distinct though interrelated hierarchical levels such that explanation at one level cannot be reduced to that of a lower level. This view has implications for understanding the relationships between evolution within populations and evolution between species.

2. Organism and environment are not dichotomous or
STRENGTH IN DIVERSITY: A READER IN PHYSICAL ANTHROPOLOGY

opposing elements, but they interact in complex ways so that the distinctions between them are often blurred. Organisms do not simply respond to environmental pressure, but their behavior plays an active role in deciding their own evolutionary fate.

Developmental processes are crucial links between genotype (the set of genes inherited by an individual) and phenotype (all aspects of the individual’s morphology, physiology, behavior, and ecological relationships). Understanding how phenotypic variations are generated and expressed is a prerequisite to the understanding of evolution.

Biological characteristics of species today are products of interaction between current and historical processes. Evolutionary interpretation of genetic, physiological, morphological, and behavioral patterns must be made in terms of the evolutionary history, or phylogeny, of the species in question.

An underlying concern here is that evolutionary theory is highly dependent on metaphors to make sense of the world. While metaphor often brings novel insights because it allows “understanding and experiencing of one kind of thing in terms of another” (Lakoff and Johnson, 1980:5), it can also lead to a reduced and distorted view of reality when the metaphor is mistaken for the actual phenomenon itself. Just as it is common to think of organism as “machine” and genetic instruction as “program”, so too there is a tendency to view “nature red in tooth and claw” as an objective representation of the organic world. “Survival of the fittest”, “struggle for existence”, “maximization”, “cost and benefits” are examples of central concepts of orthodox evolutionary theory but their original status as metaphors is often forgotten. Periodic re-examination of the conceptual tools with which we interpret the world is therefore important.

DARWINISM, NEO-DARWINISM AND ULTRA-DARWINISM

Darwin (1859) stated clearly in The Origin of Species that he had two goals: (1) establishing the fact of evolution — namely that organisms have descended with modifications from common ancestors, and (2) that natural selection is the mechanism by which evolutionary changes can be explained.

In proposing natural selection, Darwin departed from his forerunners and provided a thoroughly mechanistic causal explanation for the origin and maintenance of living things. Darwin rejected the long-held western mode of “typological” thinking, which views species as permanent and unchanging, and individual variations as inconsequential, and introduced, instead, the variational view that differences between individuals are the raw material for future change. Darwin arrived at this view by drawing on the analogous process of “artificial” selection, whereby plant or animal breeders can create desired new “varieties” from existing organisms. Darwin reasoned that small differences between individuals, accumulated over a long period of time, eventually result in the formation of distinct species. What remained to be explained was how natural selection could take place without human or divine intervention. Darwin found an answer in the political philosophy of Thomas Malthus and his model replaced the role of the breeder with the “struggle for survival.” Of this famous phrase, Darwin (1859) wrote:

I use this term in a large and metaphorical sense including dependence of one being on another, and including (which is more important) not only the life of the individual, but success in leaving progeny....

A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase. Hence as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species or with the individuals of distinct species, or with the physical conditions. It is the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdoms; for in this case there can be no artificial increase of food, and no prudential restraint from marriage. (italics mine)

According to Gould (1989:66-67), the restriction of selection to “struggle” among individual organisms was central to Darwin’s new paradigm of nature. As such, all phenomena traditionally ascribed to God’s creative power could arise as incidental consequences of nature’s only causal process — the struggle among organisms for personal reproductive success. Evolution can only take place when the variations needed to permit change at a given place and time happen to be available. Variation is, therefore, apparently due to chance because it occurs without reference to the needs of the organism in its particular environment. However, selection, the necessitating component of evolution, indirectly shapes lineages of organisms through differential reproduction in more adaptive and survival-inclined directions (Monod, 1970). Hence, features of
organisms and their behaviour that appear purposeful need not have been purposefully designed by a Creator. Natural selection could appear as a director of evolution by the combined action of the two stage process of chance variations and selection.

While the operation of natural selection is predicated on the existence of heritable variations amongst organisms, Darwin was unable to explain how such variations arose in the first place, beyond suggesting “a tendency to vary, due to causes of which we are quite ignorant” (Darwin, 1872:146). Without a firm foundation for the material basis of inheritance and variations, natural selection fell into disfavour soon after its introduction (Bowler, 1983). The confirmation that natural selection is, indeed, viable had to await the rediscovery of Mendel’s experiment at the turn of the century on the segregation of discrete factors, now call genes, as the basis for the inheritance of differences between individuals.

With the advent of the science of genetics, the origin of variations became identified with the process of mutation and recombination. However, natural selection was not initially or universally accepted by Mendelians such as De Vries (1906), William Bateson (1922), and Goldschmidt (1940) who maintained that the inheritance of large genetic differences between organisms, known as “macromutation”, was responsible for the discontinuities between species. Evolution, in their view, takes place rapidly rather than through the gradual accumulation of small differences, the latter being a fundamental presupposition of Darwin himself. In the 1920s and 30s, a group of mathematically oriented biologists, also known as biometricians, began to develop statistical models for predicting the distribution of genetic characters from the parental to the offspring generation. The works of Wright (1931), Fisher (1930), and Haldane (1932), in particular, fostered a view of evolution in terms of the steady shift of an entire population rather than the production of new forms from macromutations. Accordingly, mutations are regarded as playing “little or no creative role in evolution but that natural selection shapes adaptations out of an infinite supply of very small mutations.” (Orr and Coyne, 1992:727). To paraphrase the geneticist Monod, mutation provides the noise, from which natural selection draws out the music.

At the same time that mathematical models of genetic composition of populations were being developed came observational findings by Chetverikoff in the Soviet Union, and others elsewhere, indicating considerable genetic variation in natural populations upon which selection could act (Greene, 1981). All these studies helped establish the concept that it is the population that possesses the variability necessary for evolutionary genetic change through space and time, whereas an individual only acts as the raw material of evolution: populations evolve, not individuals.

The shift from a typological approach to what Ernst Mayr called “population thinking” gave rise to the trend, best exemplified by Dobzhansky’s (1937:11) statement in Genetics and the Origin of Species that “since evolution is a change in the genetic composition of populations, the mechanisms of evolution constitute problems of population genetics.” This emphasis on the genetics of populations helped transform evolutionary thinking into its modern form.

In addition to the rise of population genetics, a number of lines of evidence converged during the 1940s from paleontology, biogeography, and systematics that once again affirmed the status of natural selection as the principal mechanism of evolutionary change. This convergence of lines of evidence was called the “Modern Synthesis”, and is usually associated with the work of people like Mayr, Dobzhansky, Simpson, Stebbins, and many others (for an in-depth history and references see Mayr, 1982). The Modern Synthesis is often referred to as Neo-Darwinism, an appropriate name since this is essentially Darwin’s own vision of evolution. As Provine (1982:505) points out, “the new Darwinism appeared to differ from the original chiefly by addition of Mendelian heredity, field research, and an overwhelming vote of confidence from biologists.”

Mayr (1980:1) summarized succinctly the two major tenets of the synthetic view of evolution:

The term “evolutionary synthesis” was introduced by Julian Huxley in Evolution: The Modern Synthesis (1942) to designate the general acceptance of the two conclusions: gradual evolution can be explained in terms of small genetic changes (“mutation”) and recombination, and the ordering of this genetic variation by natural selection; and the observed evolutionary phenomena, particularly macroevolutionary process and speciation, can be explained in a manner that is consistent with the known genetic mechanism.

Thus, Darwin’s notion of evolution, based originally on phenotypic change, was redefined in genetic terms as “any change in the frequency of alleles within a gene pool from one generation to the next” (Curtis and Barnes, 1989:974). By extension, evolutionary mechanisms operating at the population level, usually referred to as microevolution, can also be used, by the process of extrapolation, to explain evolution at higher taxo-
strength in diversity: a reader in physical anthropology

nomic levels, that is macroevolution (see figure 1). Restated, changes on a small scale, given sufficient time, give rise to changes at higher taxonomic levels, such as those of species, genera and family. The principles and mechanisms of population genetics are then seen as both necessary and sufficient to account for all evolution (Charlesworth, 1982; Ayala, 1983; Stebbins and Ayala, 1981). Within this context, when biologists claim to have evidence of evolution, it usually means that they have detected a change in the frequency of genes in a population. As genes are passed on through reproduction, reproductive and associated activities came to be identified as the quintessential components of the evolutionary process. Mayr’s classic definition of species in terms of reproductive isolation (see Thompson, this volume, for detail), which has dominated the literature in the last few decades, is predicated on such a concern for genetic transmission. Within this gene-centred perspective, a population can be further reduced to aggregates of gene complexes tending to vary this way or that. A population is easily conceived in terms of its “gene pool”, while natural selection, random genetic drift, mutation and gene flow are considered the four primary “forces” that can cause changes in the frequency of genes within populations. Population genetics has successfully provided mathematical and predictive models for these primary forces, particularly natural selection (Hartl, 1988). This success in turn guarantees the central role of population genetics within the synthesis.

Gould (1983) notes that in the early days of the synthesis, views pertaining to evolution were rather pluralistic, but later “harden” around the adaptationist and genetic core. The decade following the 1940s saw the complete denunciation of Lamarckian inheritance (see Saunders, this volume), typological thinking, and a host of biological theories not compatible with the central tenets of the synthesis (Greene, 1981). While many biologists continue to acknowledge the fact that Neo-Darwinism is not a singular theory but a pluralistic research program with many corollary hypotheses, those who subscribe to Neo-Darwinism tend to equate evolutionary explanations with those based on natural selection (Ho, 1988).

ultra-darwinism

As population genetics theory came to dominate the Modern Synthesis, both the definition of evolution and of natural selection became more restrictive. Just as changes in the genetic content of a population have become a measure of the degree of evolution, so differential reproductive success between individuals with different genotypes has become an indication of the action of natural selection. In other words, individuals who possess a variant of a gene that accords greater advantage in competition within a particular environment will leave more offspring than those individuals who lack such a gene. Similarly, differential mortality is predicated on genetic differences between individuals. All manner of evolutionary change, in morphology, physiology, and behavior is assumed to be genetically determined. Thus, natural selection, while appearing to operate at the level of the individual, actually takes place at the genic level. All explanations depending on higher level processes such as “group selection”, according to which natural selection favours attributes that help one group compete with another, are rejected. This individual-centred view of evolution is most forcefully stated in one of the most influential evolutionary treatises in recent decades: G.C. Williams’s adaptation and natural selection (1966). Williams’ demolition of the group selectionist thinking appears so decisive, and his demonstration of genic selection so convincing, that evolutionary biologists have largely confined their explanations to the level of the individuals (Williams, 1986; but also see D.S. Wilson, 1989, 1993 for a defense of group selectionism).

Figure 1. The Conceptual Relationship Between Micro- and Macroevolution According to the Modern Synthesis

Mechanisms operating at the individual level can be extended to explain origin of higher taxa such as species. The layers on the left represent levels of detail in biological history, from individuals in a family tree, to the species in an evolutionary tree.
STRENGTH IN DIVERSITY: A READER IN PHYSICAL ANTHROPOLOGY

The conviction that all evolution occurs by natural selection acting upon individuals competing for personal reproductive success has had important, thought not necessarily a positive, impact on how evolution, and particularly of behaviour, is studied. It has created the common impression that since reproductive success must be measured in terms of the number of genes transmitted to the next generation, any behaviour that maximizes such transmission will be favoured. In addition, Hamilton (1964 a, b) showed mathematically that an organism need not succeed by means of its own reproduction; helping relatives who share enough of one’s genes may serve equally well if evolution is measured in the expanded currency of “inclusive fitness”. Fitness, in this context, depends not simply on how many offspring one has. An individual can maximize his genetic representation, or fitness, in future generations by ensuring the survival of his relatives since they carry genes in common with him. It follows that the more closely related the individuals, or the more genes they share, the more likely they will be to aid one another because each benefit from the interaction. This notion, known as kin selection, became the cornerstone of modern sociobiology that took shape in the late 1970s. Sociobiology, in turn, became a buttress of ultra-Darwinism (Eldredge and Grene, 1992), the extreme version of Darwinism that reduces the evolution of all social behaviour to differential reproductive success. Sociobiology takes behaviours (such as altruism, or self-sacrificing behaviour) that seem contrary to the key Darwinian belief in fitness maximization, and shows how they are adaptive in the service of individual reproductive success.

In the more extreme form of this reductionist thinking, known as selfish-gene theorizing, individual organisms are simply regarded as transient vehicles for carrying genes from one generation to the next (Dawkins, 1976, 1982). According to this view, individuals are thought to live in social groups only because group living is beneficial to the individuals because it provides greater protection against predators, or greater support during feeding competition with other groups. Social structure, or organization, is then seen as an epiphenomenon, varying this way or that according to the demand ecological factors place on the individuals (see review by Chan, 1992). This principle has been applied to all species that live in groups, from birds to social mammals, and from primates to human foragers (see the papers in Rubenstein and Wrangham, 1986).

Ultra-Darwinism is, therefore, a uni-causal, single level theory of evolutionary causation, with exclusive focus on differential reproduction as the source of all evolutionary explanation, meaning and content (Eldredge and Grene, 1992). As genes are regarded as the ultimate unit of evolution, the study of morphological and behavioural evolution is reduced to a search for genes. In its extreme form, sociobiological study of animal and human behaviour becomes little more than an exercise in “adaptive story-telling” based on hypothetical genes controlling arbitrarily assigned behavioural traits (see Kitcher, 1985 for a critical examination of the assumptions and pitfalls of sociobiology).

CRITIQUES OF ADAPTATIONISM AND ALTERNATIVE VIEWS

Since the 1970s, the main focus of evolutionary theory has begun to swing towards a critique of the central tenets of the modern synthesis and of the restrictiveness of ultra-Darwinism. The challenge to orthodox theory was largely initiated by the theory of Punctuated Equilibrium (the theory that evolution operates in fits and starts), proposed by Eldredge and Gould (1972), as well as by the growing reaction to human sociobiology. In an influential paper, Gould and Lewontin (1979) criticize what they call the “adaptationism program”, or the overzealous use of natural selection and adaptation as the only explanatory principle. They stress the importance of considering chance phenomena such as random genetic drift (fluctuation in gene frequency due to accident) as an alternative explanation for genetic and morphological, as well as behavioural, characters. They point out that biological form can include vestiges of selective forces no longer operating, or incidental products that are the result of developmental processes evolved under selection for other aspects of the phenotype (see explanation below). In particular, Gould and Lewontin fault the adaptationist program because of its two primary assumptions:

1. that the evolution of complex organisms, including their structure and behaviour, can be understood by the atomization or breaking down of the features into separate traits and then explaining each trait separately.

2. that the atomized characters are assumed a priori to be “optimal solutions” to the evolutionary “problems” posed by the environment.

The first assumption, in fact, rests on the mechanistic notion that the whole is simply the sum of its parts and on the belief that complex organisms can be reduced to their basic components and then reconstructed to form a whole. This approach is the corollary of the Neo-Darwinian
STRENGTH IN DIVERSITY: A READER IN PHYSICAL ANTHROPOLOGY

extrapolationist strategy of explaining all of evolution in terms of microevolutionary mechanisms. Just as mechanisms at the population level can be extended to explain phenomena at the species level or higher, so explanations at the population level can be reduced to causes at the genetic level.

In addition, Gould and Lewontin (1979) point out that according to the second assumption, similarities between organisms in morphology, behaviour, and even social systems are taken as proof of convergent ecological adaptation to similar selection pressure. The field of study known as behavioural ecology, which has become extremely popular in recent years, rests heavily on the assumption that similar social structures will result when animals, regardless of their evolutionary heritage, are faced with similar ecological conditions. In such a case the goal of research becomes an exercise in demonstrating the way in which the adaptive state has been, or will be, reached (Chan, 1992).

A subtle consequence of this mode of thinking is that the individual organism is treated as a passive entity subjected to external forces. Individuals are driven by genetic predisposition to maximize their reproductive output, and the variants that leave the most offspring in a particular environment will be best represented in subsequent generations. Organisms play little or no role in their own evolutionary fate.

The assumptions underlying the adaptationist program suffer from four major flaws: they ignore the hierarchical nature of biological organization; they deny any active role to individuals in the evolutionary process; they fail to acknowledge the constraints of existing morphology and do not take into account the historical origins and path of the evolutionary characters to be studied.

(1) Importance of the hierarchical concept of biological organization and causality

Since evolution occurs at various hierarchical levels, the reductionist explanation of phenotypic phenomena, which is restricted to events at the genic level, is clearly inadequate (see Figure 2). As an example, the relation of gene and protein molecules may be considered. The information concerning the linear composition of protein molecules is stored in the structured gene. However, once the protein molecule has been assembled from its constituent amino acids, it spontaneously folds to assume its functional three-dimensional conformation. While the physiochemical principles governing the folding are not fully understood, it is clear that the folding instructions are not stored in the DNA sequences. This implies that the information concerning the folding rules represents a higher level of organization than that represented by the linear amino acid sequence, and that folding rules may be level-specific organizing relationships that cannot be deduced from the DNA molecule. This example, although simplistic, illustrates that when higher level integration and organization are involved, it is misleading to talk of "mapping" or "translation" between levels (Rose, 1981). If a direct mapping between the DNA nucleotide sequence and the three-dimensional structure of protein molecules is questionable, then the one to one mapping between genotype and phenotype are far more problematic (Lewontin, 1992).

Thus, organisms cannot be reduced to a sum of genes, nor societies to a sum of individuals. The latter is not only true for humans, but also for all animal societies. For example, ant colonies exhibit recurring patterns of group behaviour such as foraging and defence that are not apparent at the individual level (Gordon, 1988). Furthermore, research by primatologists reveals that social systems in non-human primates emerge as a consequence of the interaction between individuals for a multiplicity of reasons unrelated to reproduction (Rowell, 1983, 1988). Social traditions arise as a consequence of the social networking between individuals, and the individuals are, in turn, restricted or facilitated by the traditions within which they live (see Burton, this volume). Social tradition, in Burton's view, serves as the repository of social and ecological information pertinent to the maintenance of the group, and tradition therefore constitutes higher level phenomena independent of the individuals comprising the group. Thus, there are level-specific regularities that should be investigated in their own right, and more importantly, these regularities constitute parameters that can determine the behaviour of the constituent parts. In his study of the Rendill, pastoralists of northern Kenya, Roth (this volume) illustrates how an understanding of the complex relationship between social rules, which affect the individuals, and demography, which is measured in group terms, depends on knowing how factors at the group level influence outcomes at the individual level and vice versa.

The strongest objection to reductionist and extrapolationist thinking, therefore, is that there is no direct rule of translation from one level of the biological hierarchy to the next 'down' or 'up' (Eldredge and Grene, 1992). Explanations that may be appropriate at the individual level may not be adequate at the population level. Changes in gene frequency do not always parallel changes in morphology or life histories characteristics,
such as longevity and gestation length. Likewise, changes in life history traits or morphology do not necessarily imply changes in genetic components. Molecular biology has also shown that at the genic level, many mutations are neutral; they are neither selected for nor against, and occur at approximately constant rates over the course of evolution (Kimura, 1983). Morphological evolution, on the other hand, occurs at a much more uneven tempo, with long periods of “stasis” or no change, punctuated by relatively rapid bursts of major changes associated with lineage splitting or speciation (Eldredge and Gould, 1972; Gould and Eldredge, 1993). The prevalence of discontinuous changes at different levels reinforces the recognition that accumulation of selection within populations over time may be entirely inappropriate as an explanation for novel features and diversity (Vrba, 1989).

Figure 2. Causal Relationships Between Levels of the Biological Hierarchy

The two-way causal processes, shown as solid line, occur between various levels of the biological hierarchy. Note that new level phenomena, namely behaviour and social tradition, emerged and mediate between lower and higher levels.

Changing Conceptions of Evolutionary Theory

(2) Organisms as active agents of evolutionary change

Organisms are neither passive objects driven by genes from within nor simply reactors to environmental pressure from without. In addition, it is overly simplistic to characterize behavioural development as the complex interaction between nature and nurture. As Rose et al. (1984) point out, the organism and environment “interpenetrate” in such a way that there is, in fact, no such thing as organism and independent environment. Lewontin and colleagues maintain the term “environment” does not refer to the external physical world as a whole. “Environment”, from the point of view of the organism, means the surroundings as defined by the organism itself. Therefore “there is no environment without an organism” (Rose et al., 1984:273). Similarly, as Groves (1989:33) remarks,

...animals do not merely live in an environment and await mutations that may make them better adapted to it: to a surprising extent they select their own niches and their own habitats. It is surely not such an outrageous claim to make that animals, rather than being adapted to an environment because they live in it, may live in an environment because they are adapted to it.

Organisms respond to a “problem” imposed by the environment, but in their response they change the nature of the problem itself. This process referred to as “reciprocal constructivism” by Gray (1988) is a process increasingly recognized by students of behaviour and evolution (see for example Oyama, 1985, 1989; Kitchell, 1990, Bateson, 1988; Hailman, 1982; Lewontin, 1983).

The process of reciprocation between environment, both social and physical, and biology has probably been the most prominent in the course of human evolution, as humans have continously redefined their relationship with the environment. The evolutionary “problems” that confronted our ancestors did not stay the same, and the solutions to them were apt to change. More importantly, however, when evolution is driven by features of the social structure of the evolving species, the process transforms the evolutionary context of the evolving organism. The evolution of language, tool use, complex systems of reciprocity, and of peace making, are not solutions to a set of pre-existing problems facing the human organism. Indeed such “solutions” may, in the course of social evolution, themselves pose new problems that demand further resolution. Thus, behavioural changes set the stage for further evolutionary reciprocation between
organisms and their environment, and propel organisms in directions that might not be predictable using purely adaptationist assumptions. There are no pre-defined problems "out there" to which natural selection can fashion stable or invariant solutions (Lewontin, 1983); the organisms and their behavioural repertoire have the final control over the outcomes.

Despite the central importance of human behavioural complexity, the majority of models of how we became humans continue to depict early hominids either at the constant mercy of the harsh tropical African savanna, or embroiled in the incessant struggle for fitness maximization. So bipedalism, a unique evolutionary trait, is often seen as a solution to the various "problems" of "predator avoidance", or "food gathering", or "long distance travelling", or "heat stress" (see the recent review by Jablonski and Chaplin, 1993). Clearly, we need to rethink our entire conceptualization of the interrelations of the human organism and the environment and, in the process, develop a new approach to the entire question of "internal" and "external" causes in evolution.

3) The Importance of Developmental Constraint

Organisms are not collections of atomized parts, each separate and distinct. Change in one part of the organism may entail correlated change in others, often for structural and developmental reasons unrelated to current adaptation. This phenomenon is true at the genic as well as at the organisinal level. Because genes reside on the chromosome, selection for a particular gene often results in the "hitch-hiking" of neighbouring genes that reside on the same chromosome. Thus, the phenotypic effects associated with the hitch-hiked genes are not necessarily those selected for (Lewontin, 1986).

At the phenotypic level, many characters are tightly integrated and are passed on as an integrated suite. Selection of one component of the suite may result in the replication of the entire suite. Thus some components are non-selected though they are also heritable. A case in point is the presence of male nipples, which clearly serve no adaptive purpose. Their presence makes sense because "males and females are not separate entities, shaped independently by natural selection. Rather the two sexes are variants upon a single ground plan, elaborated in late embryology" (Gould, 1987:16). Males nipples are a functionless homologue, character inherited from a common ancestor, maintained because they are a necessary outcome of the developmental sequence that results in female nipples. Developmental biologists thus caution that before we propose an adaptationist hypothesis for a trait, we must first understand how the trait or structure is assembled.

In addition to the tightly integrated nature of some structures, developmentalists also recognize that certain characteristics exhibit long term stability, referred to as "stasis", while some are extremely labile and prone to change. An organism is made up of features of varying antiquity, and some traits appear to evolve relatively independently of the rest of an organism's phenotype. Human morphology embodies many such characteristics; our dental pattern is some 35 million years old, and our tail bone was formed 25 million years ago, while our elbow joint was shaped only 15 million years ago, and our bulbous cranium is a mere 0.10 million years old (Lewin, 1989:78).

The question then becomes why are certain features so resistant to change, and what implications such "stasis" has, especially with regard to the generation of variations and novel features. The answer lies in part in the observation that not all possible morphologies exist for any given body plan (Alberch, 1982, 1990). (There are no flying monkeys, and there are no four-eyed mammals with two heads). So while nature's diversity appears to be boundless, there are, in fact, limits as to what could possibly evolve. Unlike adaptationist thinkers who ask why animals have this or that feature and how it functions in terms of promoting reproductive success, developmental biologists are interested in why one particular form evolves instead of another that might be just as well, or even better, suited to the current environmental problem. This mode of evolutionary questioning has been largely ignored until recently, since evolutionary biologists have traditionally focussed on the issues of change and variation, rather than on stasis and limited possibilities (Wake, 1991; Gould, 1989; see also the various papers in Wake and Roth, 1989).

Developmental biologists interested in constraint or limited possibility are concerned with rules of internal organization, according to which form precedes function, and with the hypothesis that a set of basic body plans of organisms underlie the diversity of organism observed in nature (e.g., Seilacher, 1990; Alberch, 1990). Primate species are highly diverse in external appearances and in genetic makeup, but they all share the same skeletal structure, albeit in varying proportions. In particular, developmental biologists point out that the development of organisms is an intricately orchestrated and highly conservative process. This process may restrict the amount and direction of variation so that the material available to natural selection is not random, and hence, the channel of evolu-
tionary change is, in part, determined by developmental parameters that limit possible variations. To the extent that variation and evolutionary direction are strongly constrained by internal rules of organization, the rule of natural selection as a creative and directing force is simultaneously diminished (see Figure 3).

Figure 3. Relationship Between Ontogeny, Development of the Individual, and Phylogeny

Developmental parameters may be fixed early in a species phylogeny and constrain subsequent diversity. Adaptation, in this context, is seen as recent modification of variations already shaped by development.

Diversity, rather than being generated by chance and necessity, is the result of variations on a common theme. The existence of a theme, or repeating pattern, implies the existence of internal constraint, which in turn allows us to question the scope of possible innovative variation (Muller, 1990). Neo-Darwinians tend to see selection as an opportunist—a "tinkerer," to use the eminent French biologist François Jacob's (1977) term—trying to make the best out of whatever is available. Developmentalists, on the other hand, tend to see the transition between morphological forms as the evolution of the "tolerable" rather than the optimal (Hallman, 1982). But as Wake (1991) points out, the two positions, although defining different methods of analysis, are in fact complementary. Organisms are the embodiment of the past and the present, living in a world of "opportunity within constraint" (Albrech, 1990), being, at the same time, both similar and different from one another. Understanding this paradox is indeed the primary purpose of evolutionary theory. Darwin's great insight was that sameness derives from common descent, while differences arise from modification through selection. The study of evolution is, fundamentally, a study of historical sequence of events, leading to the distribution of novelties and sameness through space and time. Thus, members of the same species share a common evolutionary history distinct from that of other species (Cracraft, 1990). Subsequent evolutionary changes are restricted within the bounds set by the species' history. Understanding of the current adaptation of a species, therefore, calls for an understanding of its evolutionary history or phylogeny (Brooks and McLennan, 1990).

4) Evolution as an historical science

Population biologists, although often acknowledging the impact of history, tend to think in ahistorical terms. Most of population genetics, the adaptationist program, and much of behavioural ecology are built on the assumption that the populations under study are in, or are rapidly approaching, equilibrium. That is, the current state of the organism or of the population is the same as it was in the past (Lewontin, 1986). A further assumption is that the current environment is the same as that in which the population evolved. According to this view, to understand the current function of a particular character is to uncover the evolutionary reason why the character evolved.

The assumption that the population is in equilibrium is misleading, however, because as Lewontin (1974) persistently points out, "equilibrium annihilates history". The evolutionary mechanisms that act on any population do so within limits set by the population's history, but this history is obscured if the population is assumed to be in stable equilibri-
STRENGTH IN DIVERSITY: A READER IN PHYSICAL ANTHROPOLOGY

um. Gould and Lewontin (1979) also caution against explanations involving adaptation when the history of a lineage may offer better clues to the current state of affairs. Equally important is the need to distinguish functional explanations from historical or evolutionary questions about origin. For example, there is little doubt that our lungs are highly functional and are, in fact, an important adaptive feature. Yet, it would be senseless to propose an adaptive hypothesis for the number of lungs we have, because the number of lungs is a consequence of the general bilateral symmetry of our bodies and of the developmental mechanisms controlling that symmetry. Bilateral, symmetrical development is a characteristic of the chordate line and there may never have been any variation in its number of lungs. In other words, bilateral symmetrical development sets severe limits on the action of selection. Hence, many features associated with bilateral symmetry remain stable over the course of evolution.

Stearns (1992:94) points out that "the basic design common to a higher taxon shapes the rough boundaries within which the life cycles of all its constituent species evolve." Likewise, many life history traits are invariant at high taxonomic levels (such as Class and Order), and show no variation between populations, while other traits appear fixed at lower taxonomic levels (such as population and species). All birds lay eggs and none give birth to live young; all mammals nurse their young with milk; all primates have an egg supply of approximately 50 years; and most human females experience menopause at a similar age (Fedigan and Pavelka, this volume). On the other hand, many life history traits are highly variable. For example, the degree of parental care varies widely across mammalian species; although most primates give birth to one offspring at a time, intervals between births vary not only between primate species, but also between populations within species. The recognition that certain traits are invariant at high taxonomic levels while others are highly labile serves as an important reminder that historical and developmental constraints are important components of the evolutionary pathway, and so phylogeny must be taken into account when one compares life history parameters across species.

Until recently, adaptationists have largely ignored the role of history or phylogeny, and have overlooked the origin of the traits under study. Without knowledge of the origin of a trait in relation to the organism's phylogeny, it is impossible to ascertain whether the feature first appeared in the species' current environment, or in an ancestor exposed to quite a different environment. Such information might indicate that the trait is "primitive", and shared by a broader set of species belonging to a higher taxonomic level. Consequently, without taking into account phylogeny, it is easy to make the mistake of proposing an adaptationist explanation for a trait when none is needed.

To circumvent this problem, many researchers have adopted phylogenetic methods to try to tease apart the origin of characters from their functional maintenance. One approach consists of establishing genealogical relationships between species first, and then asking if similar traits arose in a common ancestor and have persisted, or if they arose independently due to convergent adaptation. This approach, referred to as the comparative phylogenetic approach, emphasizes the importance of a species' evolutionary history in constraining the features it currently displays and the subsequent directions and rates of evolution open to it (Huey, 1987; Lauder, 1986; Dobson, 1985; Watneorp, 1983). These features include phenotypic, behavioral, as well as ecological, characteristics. By mapping these features on a well established cladogram, a branching diagram of how species are related to one another, one can estimate when, and how many times, an observed characteristic arose in the group under studied. One can also gain some insight as to what features tend to co-evolve, which features are highly conservative, and which are most labile. This approach emphasizes that adaptationist explanation is only appropriate once the hypothesis that the observed similarities are due to common descent has been rejected (Coddington, 1988). This mode of reasoning in terms of phylogeny, which O'Hara (1988) referred to as "tree thinking", is one of the most important conceptual developments in recent years. Tree thinking is having a substantial impact on the study of ecology and behavior of a wide range of organisms (see Brooks and McLennan, 1990; McKittrick, 1993; Miles and Dunham, 1993, and references therein), although its effect on the study of human social evolution has not yet been fully explored.

CONCLUSION

Since the triumph of the Modern Synthesis, the concept of natural selection has been accorded a priori status. The philosopher of biology, Marjorie Grene (1981), coined the phrase "the axiom of adaptivity" to refer to the belief that most major features of living things are functions of the need to adapt to environmental circumstances, a belief that is so deeply-seated that it is scarcely ever mentioned. The popularity of natural selection as an evolutionary explanation also leads to the false impression that
adaptations dominate evolutionary change both in frequency and importance. But the real appeal of Darwinism does not lie in its ability to explain organic diversity, but in the set of metaphors it offers. The notions of "struggle for survival", "survival of the fittest", "maximization", reproductive "strategies" are very powerful metaphors and reinforce a utilitarian perception of nature deeply ingrained in capitalist societies. These metaphors also reinforce the idea of competition and strife at the expense of all other human qualities, such as cooperation and mutual care. For decades, the notion of competition has been seen as the central principle in the structuring of ecological communities, so much so that other important phenomena such as mutualism and cooperation have been largely ignored. It now appears that the power of competition in maintaining species relationships has been vastly over emphasized and the empirical support for the phenomenon is highly dubious (Keller, 1988), while mutualism and cooperation are far more common than previously supposed (Margulis and Sagan, 1986; Thompson, 1988; Vandermeer, 1980; Simberloff, 1983). Yet, competitive exclusion continues to dominate discussion of species interaction in non-human primates (Burton and Chan, in press), and subtly underlie the so-called "Replacement" hypothesis of modern human origins (see Willoughby, this volume). Nevertheless, Mayr (1994:337), the last living founder of the Modern Synthesis, continues to declare that "every property of any living organism has evolved with the assistance of natural selection." Old views tend to die hard.

There have been substantial changes in the field of physical anthropology in the last three decades, becoming with the dismantling of the "man the hunter" model of human evolution in the 1960s, followed by the deconstruction of culturally and politically biased narratives of human evolution (Wolfe, 1991). At the same time, however, the theoretical framework within which human diversity and uniformity are being interpreted remains substantially unchanged and continues to retain an orthodox Darwinian core. I hope to have offered some critical reflection on the shortcomings of existing views about evolution and in so doing to challenge the readers to broaden their existing concepts about origins and develop alternative and pluralistic metaphors that better represent nature and our place within it. Evolutionary theory is a powerful and unifying framework for all biology, but it is also a theory that, itself, is continuing to evolve. We risk promoting theory into dogma if we fail to critically question existing views.
STRENGTH IN DIVERSITY: A READER IN PHYSICAL ANTHROPOLOGY

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Changing Conceptions of Evolutionary Theory

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