

PALEOSCENE #4. Darwinian Evolution and Developmental Biology: A brief review of current ideas

Lars E. Fähræus
Department of Earth Sciences
Memorial University of Newfoundland
St. John's, Newfoundland A1B 3X5

"Nature always begins by resisting the artist, but he who really takes it seriously does not allow that resistance to put him off his stride; on the contrary, it is that much more of a stimulus to fight for victory, and at bottom nature and a true artist agree." (Vincent van Gogh, 1881, quoted from Bernard, 1985).

Introduction

The Darwinian theory of evolution is presently experiencing a thorough shake-up. It is being critically looked at from several angles, epistemologically as well as with regard to its empirical foundation.

Most major scientific theories are, from time to time, subjected to revitalization in the form of new ideas resulting from breakthrough scientific discoveries. However, interestingly enough, in the case of the Darwinian theory of evolution it is not exclusively new ideas that are stirring this shake-up but also many old ones, some would say skeletons, that are brought out of the closet, dusted off, and equipped with new guises in the form of rigorously scrutinized modern laboratory and field data. Even the approach to evolutionary study is in many instances reverting to that of the pre-1950's, i.e. it is again becoming typological, being focussed on the individual, rather than the population approach which has dominated evolutionary biology for more than three decades. Today we find that the most exciting approaches to evolutionary theory are again made in experimental embryology or epigenetics with a large input from molecular genetics and biochemistry; areas of study collectively referred to as the science of Developmental Biology. There is also a grudging but steadily increasing acceptance of the possibility that the fossil record, poor as it may be, represents a rough but true picture

of the course of evolution (Stanley, 1979). All of this has led to scientific discoveries and considerations that many believe to be incompatible with a strict adherence to the Darwinian concept of evolution.

In the present article I am trying to summarize what is currently happening in the realm of evolutionary theory. Some of the ideas put forward in this exposé, I am sure, will be considered controversial but, if nothing else, they will provide some food for thought. And that, after all, is the general purpose of this review article.

If we disregard for the moment the current vigorous discussions centered around the Eldredge and Gould (1972) "punctuated equilibria" theory (i.e. that evolution is characterized by bursts of morphologic and physiologic diversions, followed by long intervals of evolutionary stasis) — which in many ways has served as a catalyst and point of departure for theoretical excursions into the more fundamental aspects of evolution — much of the current discussion is concerned with two issues: (1) the role of natural selection in evolution, and (2) the processes governing the translation of the genetic information into the realized phenotype.

This discussion deals with two levels of evolution: micro-evolution at the species level and macro-evolution at the supra-specific level. Micro-evolution we can envisage as the more or less gradual transition of one species into another. Macro-evolution, on the other hand, tries to explain the successively larger morphological and physiological gaps that can be observed among organisms as one proceeds from genus to family to order to class, etc.

The Darwinian theory of evolution relies on three indisputable facts: (1) all organisms produce more offspring than the environment can support, (2) heritable variations do occur, and (3) the existence of a non-static environment producing ever-changing demands on the organism.

Based on these three premises Darwinian evolutionary theory, simply stated, proclaims that evolution from one species to another and, most importantly, to higher taxa, proceeds in slow, almost imperceptibly small steps. The raw material includes accumulations of randomly occurring (micro-) mutations with very slight beneficial effects, recombinations of available (in the gene pool) genetic material, genetic drift and, perhaps, so-called meiotic drive. The guiding force is natural selection which weeds out the poorly adapted individuals and promotes those that are the "fittest to survive". Neo-Darwinism, emerging in the latter half of the 1930's and vigorously promulgated in the 1940's, added the genetic aspects of this theory. Neo-Darwinism argues that there is no fundamental difference between micro- and macro-evolutionary processes. Opposers, on the other hand, argue that there is a fundamental difference between those evolutionary pro-

cesses taking place at the species level and those occurring at the supra-specific level.

Darwinism or neo-Darwinism has come under increasingly heavy fire during the last decade from several quarters: (A) it has, as a theory of evolution, been considered non-scientific (this accusation, with which I disagree, I will not discuss in this essay — the interested reader is referred to, e.g. Bethell (1976), Gould (1976), Peters (1976), and Brady (1979)); (B) evolution, at least at the species level, does not proceed in "slow almost imperceptible steps"; (C) mutations are not random and genes do not act independently; (D) functional adaptations (morphological, physiological, etc.) are not primarily fashioned by natural selection; and (E) the whole concept of Darwinian evolution is permeated by teleological thinking (i.e. that evolutionary developments occur because of the purpose or design that is served by them).

Apart from the philosophical points (A and E), this criticism largely boils down to a non-acceptance of the thesis that evolution at all levels of morphologic and physiologic organization should be the result of the combined effect of micro-mutations (i.e. small, randomly occurring and borderline beneficial mutations) and natural selection through the process of continued adaptation to the environment. In the following I will outline, and briefly discuss, some of the more salient facts supporting these criticisms.

Darwinism and Victorianism

The major tenet in the Darwinian theory of evolution is the slow gradual progression of the process. With regard to this emphasis on a very gradual progression of the evolution from one life form to another, we should remember that Charles Darwin had no concept of the importance of mutations and the Mendelian laws of inheritance, but believed in a strictly regulated proportional blending of ancestral characters: Galton's Law of Ancestral heredity. Since ancestral characters would be suppressed only slowly by new characters the very nature of such a process of inheritance of characters demands a slow step-by-step progression of the transformation from one species to another. Darwin also envisioned natural selection as a hand-maiden scrutinizing each feature individually but making no wholesale decisions. With such an outlook it is obvious that evolution had to be envisioned as a slow and very gradual process (I wish to stress this point since the purpose of this essay is not to debunk Darwin and his 1859 contribution — which in many ways was considerably ahead of its time).

This is not to say that Darwin totally excluded other causes of evolution. With regard to certain structures in plants and animals, for example, he wrote that: "... modifications of structure ... may be wholly due to unknown laws of correlated growth, and without being, as far as we can see, of the slightest service to the species"; here he was

considerably more advanced in his thinking than some of his present-day followers.

Apart from their unwillingness to accept modern data from epigenetics (experimental embryology), molecular genetics and paleontology, one of the main problems with the adherents of today's brand of Darwinism is that the terminology has not been modernized; too often it is still couched in Victorian phrases that appear, at least, to be based on Victorian thinking. The main problem being the persistent use of the word "adapt", and its derivatives, which carry with them the implication that evolution has a purpose, i.e. creating the perfect organism for the particular environment it happens to inhabit.

Teleology means that development of a biological design (morphological, physiological, etc.) is due to the function or purpose of that particular design. That is, our hand looks the way it does because its purpose is to hold and grasp; we are not holding and grasping because of the design of our hand. The fish is streamlined because it is meant to be a good swimmer, it is not a good swimmer because it is streamlined, etc. The logical consequence of such a doctrine is, of course, that the purpose is first decided upon and the design (development) comes second. Or, in other words, the end product is premeditated and the evolution toward this end product is guided at all turns. If we put it in those terms I think many would agree that such a notion is ridiculous and that evolution does not work in such a fashion. If it did, it would be dangerously close to Lamarck's generations of (to be) giraffes wanting to reach the upper branches of an African acacia and eventually succeeding.

So, teleology is ridiculous? Let us rephrase what I just said: the hand is perfectly *adapted* to holding and grasping and the streamlined fish is perfectly *adapted* to be a good swimmer. That sounds a little bit more familiar, doesn't it? In fact, Darwinians always talk about organisms as being adapted to their specific environments — a notion that obviously implies that the organism, during the course of many generations, changes to suit or fit a certain function and/or environment.

Because of its emphasis on adaptations caused by the creative force of Nature, it has been said that Darwin's *Origin of Species* is a "sermon on teleology". Again, in the light of the cultural and scientific environment of the Victorian Age, this is perhaps to be expected. But what is not to be expected is the persistent usage of teleological expressions found among many present-day followers of Darwin.

Let me cite just one example. In a recent advanced text on *Form and Function in Birds* (King and McLelland, 1979) the following statements (p. 87 and p. 89, respectively), among others, can be found with regard to bill shapes: "In *Anastomus* (storks) a gap exists in the closed bill between the distal parts of the upper and lower mandibles except where the tips are opposed. . . . The gap. . . is an adaptation for securing slippery water snails"

and "The distal portion of the bill in the Wrybill (*Anarhynchus frontalis*) is bent to the right in adaptation for seeking out insects under stones". If these statements are supposed to mean that these birds found a use for their peculiarly shaped bills and the birds thus adapted to certain feeding habits then I would agree. But that is not exactly the implications that the sentences carry with them.

Let me take one example of a "perfectly adapted" organism that, from the time of Charles Darwin himself, has been cited many times in the Darwinian literature on evolution — the woodpecker, and let us see how it "adapted" to its environment (Figure 1).

The woodpecker has built-in "shock-absorbers" in the neck and head that allow it to whack away at a tree trunk with a speed and force that would leave any other bird with severe brain concussions. The nostrils are covered by bristles, presumably to keep out the "saw dust" caused by its pecking. It has a

very long retractile "sticky" tongue, made even longer by uniquely fashioned extensible hyoid bones, with which it can retrieve bugs from deep within the crevices and cracks that the pecking expands. Its feet have two toes facing forward and two toes facing backward (the three-toed woodpecker is a seldom seen exception), facilitating a secure grip on the tree trunk, and it has very stiff tail feathers functioning as a prop when pecking or climbing.

The woodpecker is certainly a perfectly adapted bird but it is more than difficult to imagine these adaptations being developed in concert through the accumulation of numerous random micro-mutations, and with the entire process being guided exclusively by natural selection.

It would seem considerably more probable that these adaptations happened through a series of a few (probably rather minor) unrelated mutations leading to modifications of certain phenotypic expressions (probably



Figure 1 The perfectly adapted woodpecker. A classical example of Darwinian evolution. See text for discussion.

accompanied by "canalization" of some eco-phenotypic features; see below) and the poor bird trying to do its best with whatever equipment possessed. The point is that organisms do not slowly adapt to a chosen environment, but find an environment that fits or suits the equipment they have; if they cannot find it they die. This particular bird, the woodpecker, succeeded; scores of others did not.

Even if we view organisms as conglomerates of morphological features caused by mutations, gene recombinations and epigenetic factors (see below) resulting in more or less new innovations looking for ecological niches where they can survive and eventually prosper, we will still have to give natural selection a very important role as the weeder of the poorly fit individuals. But it is not, however, the primary force shaping the organisms and the creator of new taxa that we are led to believe by Darwinism. Rather, it hones and fine-tunes the organism to the particular environment it has chosen to settle in. In the case of the woodpecker, natural selection would favour many of its features and improve on them, but those features that characterize the woodpecker ("Shock-absorbers", stiff tail-feathers, long retractile tongue, etc.) came about through other factors and processes which were acting both intrinsically and extrinsically; if we argue that they didn't, we are again back to teleological thinking.

In the last few paragraphs I am not only making a point but I am also trying to hammer it home using phrases that might sound like debunking the organism's power to adapt to the environment, an impression it is not my intention to convey. (In fact it is this power to adapt that might be responsible for a large part of observable evolutionary divergence at the species level.) What I am hammering at is the Darwinian theory that *all* of evolution can be explained by the combined effect of micro-mutations and natural selection through the process of continued adaptation to the environment. The point being that much of what we can see having taken place in evolution, particularly at transitions between higher taxa, is the result of factors and processes that are not directly ascribable to micro-mutations and the extrinsic environment.

Jacob (1977) has expressed much the same views: "Natural selection has no analogy with any aspect of human behavior. However, if one wanted to play with comparisons, one would have to say that natural selection does not work as an engineer works. It works like a tinkerer — a tinkerer who does not know exactly what he is going to produce but uses whatever he finds around him, whether it be pieces of string, fragments of wood, or old cardboard; in short, it works like a tinkerer who uses everything at his disposal to produce some kind of workable object."

In fact there are many examples that illustrate the fallacy of adhering to a non-critical view of Darwinism, and thus teleology. For example, think about the transition from the

anamniote (lacking foetal membrane) to the amniote (with foetal membrane) egg. In comparison with the anamniote egg, the amniote egg is a very complicated structure but, according to Darwinism, this structure should have developed through a series of random, marginally beneficial, micro-mutations with natural selection picking the right ones suitable for the final product. If this process is supposed to have taken place "in slow almost imperceptible steps", how did the intermediate generations manage? There is no way that we can imagine an organism being able to reproduce with the aid of a partially amniotic egg; the difference between the two is far too great both morphologically and physiologically; not to mention the totally different environmental requirements. Taxonomically we are speaking of the transition from one class to another — a very high level.

Hopeful Monsters

The very nature of the diversity of extant and past organisms virtually demands a belief in large-scale organic innovations and morphologic transformations and in their viability and importance for the evolution of life. If we accept no such gaps in evolution, then we would expect to find much more of a morphologic continuum among known organisms with "smooth" morphological transitions between taxa, but instead, among living organisms, we find a very well expressed graduated scale from numerous small to a few very large morphologic/physiologic gaps. Gaps that make it possible for us to order organisms in the classical Linnean classification hierarchy or in the affinity index generated phenograms of the numerical taxonomists.

The traditional answer to this observation is that the gradual transitions took place a very long time ago and that since then, divergent evolution has been at work causing an increase in the morphological gap between ancestor and descendant. And to this, of course, we have to add the proverbial deficiency of the fossil record: conveniently causing all forms showing a supposedly gradual transition at the generic and higher taxonomic levels not to be preserved, or at least not to be found, but leaving us with numerous very well documented evolutionary lineages at the species level. Surely, we do not have to stretch our powers of deductive reasoning too much in order to realize that something is at fault with this kind of argumentation.

Macro-mutations, with resulting "hopeful monsters" making the transition from one higher taxonomic level to another in one giant step, as heralded by Richard Goldschmidt (1940) and Otto Schindewolf (1936) — the latter arguing that the first bird came out of a reptile's egg — have generally been relegated to the realm of metaphysics. However, renewed interest in, and support for, the

evolutionary importance of "hopeful monsters" have come from many quarters (e.g. Steenis, 1969; Frazzetta, 1970; Busch, 1975; Stanley, 1979; Gould, 1977b, 1982).

Two of the methods Goldschmidt (1940) considered possible for the creation of hopeful monsters have recently been exposed to the limelight. Goldschmidt argued that even very minor changes in the genome could result in major changes of the developmental patterns of an organism during embryogenesis (i.e. the development from a fertilized egg to an embryo), a mechanism we can refer to as epigenetically enhanced micro-mutations; this process is discussed later in this essay. Goldschmidt also argued for karyotype (chromosome number and arrangement of genes) rearrangements as a major source for the necessary genomic variation; a process that recently has been forcefully supported by White (1978) and is discussed below.

Many studies have shown that a large part, perhaps the major part, of the DNA (i.e. deoxyribonucleic acid — the protein carrying the genetic information) in the eukaryotic genome has no phenotypically expressed coding effect (see Dover, 1980, and Dover *et al.*, 1981, for references). Much of this non-coding DNA occurs as distinct groups or families which are interspersed between and within the genes. Studies have also shown that these "families" fluctuate in size and position. In other words, the genome is architecturally quite unstable and fluid and subject to many, and frequently quite drastic, rearrangements, including growth of chromosome segments (Dover *et al.*, 1981). However, even though there is much fluctuation in size and position of these repetitive sequences, they are generally conservative in composition and survive phylogenetically longer than single copy sequences (Britten, 1982) and, even though there is apparently a state of flux in the eukaryotic metazoan genome, it is very conservative with regard to number of phenotypically expressed body-plans.

Because of this stability in the number of body-plans, it has been suggested that these repetitive non-coding sequences might combine into an interdependent network that has a regulatory effect on the phenotypic expressions of the structural genes, and that new taxa should arise through the changing of the positions of the families of repetitive sequences and through the addition of new families through time (Britten and Davidson, 1969; Davidson, 1982). That is, the impetus for creation of new taxa should be driven by intrinsic factors working on units of non-coding DNA sequences rather than randomly occurring point mutations (i.e. affecting individual genes and creating alleles).

With regard to the creation of new taxa and evolutionary divergence, Dover and co-workers (1981) have expressed similar ideas but with less emphasis on the regulatory effects

and more on the differences in abundance of shared families of repetitive sequences. These quantitative differences are considered to reflect evolutionary divergence.

It should also be stressed that the structural genes (those coding for proteins) apparently spontaneously confine themselves to a very limited number of phenotypic expressions which are very closely co-ordinated both mutually and hierarchically (Dawid *et al.*, 1982); a co-ordination that is executed not only by the regulatory genes but also by epigenetic mechanisms (see below). What this means is that the groupings of genes into gene families are caused by intrinsic factors and thus not directly a result of natural selection (Dawid *et al.*, 1982). Furthermore, the fact that regulatory gene families of largely similar composition occur among phylogenetically diverse groups might be the reason for the relatively limited number of body-plans encountered in the living world.

Experimentally well-supported data from molecular genetics thus appear to support theories about evolution that would make possible a Goldschmidian macro-mutation creating a hopeful monster.

The problem with macro-mutations is generally considered to be two-fold: (1) the resulting monster is totally "out-of-synch" with the environment of its parents and (2) it is reproductively isolated from everybody else.

In the case of reproductive isolation we should first of all remember that morphologic difference does not necessarily have to equate with reproductive isolation and *vice versa*. This has been illustrated by experimental studies on interspecific hybrids of the fruit fly *Drosophila melanogaster* where the hybrid sterility is due to incompatibilities in the germ-line and not in the soma, and, also by sibling *Drosophila* species which show few morphological differences but for the germ-lines (Dover *et al.*, 1981). More generally we have to consider the magnitude and type of monstrosity, i.e. how far can we take morphological/physiological alterations and still maintain enough reproductive capability to produce an F₁ generation — after that we can resort to inbreeding. Perhaps, it is wise to remember that more than one monster can arise by the same process. With regard to the monster being an environmental misfit, we have to consider the type of organism and degree of monstrosity. We also have to determine how, and to what degree, the monstrosity would alter the environmental requirements of the organism in question. If the monstrosity itself opens up new ecological niches within the general ecological realm of the parents then obviously the argument is nonsense.

In short, there are many opportunities for a "monster" to be able to survive and reproduce. After all, in order to explain present-day diversity, not that many opportunities are needed considering the relatively few radically

different body-plans that are known. At the genus and family levels most monstrosities would be relatively minor and, by and large, morphological in character. At the species level micro-mutations, gene recombinations, genetic drift, etc. are probably sufficient to explain most evolutionary divergence. However, as I have indicated above, we might not even have to resort to macro-mutations caused by karyotypic rearrangements in order to explain large-scale, or systemic, evolutionary gaps.

Organic Diversity

The largest stumbling block by far for Darwinism is the degree of biochemical and morphological diversity encountered in the living world. This diversity is far too limited if we seriously are to consider a model that relies on randomly distributed point mutations on a genome that consists of millions (in a bacterium) or billions (in Man) of nucleotides; never mind the rate at which they occur and whether the genome has a 20-80% redundancy or not. A few numbers taken from Smith and Morowitz (1982) will show the size of this stumbling block.

In a metabolizing cell we find about 20 specific amino acids, polymers of four ribonucleotides and four deoxyribonucleotides, polymers of a few sugars and a few lipids. In fact, if we look at the total living world, we will find that about 90% of all living substance can be accounted for among some 50 to 100 specific molecules and their polymers. On the other hand, if we calculate the possible number of proteins 100 amino acids long, assuming that only one in a million is water soluble and that only one in a million of those will have a chemically active surface, we still come up with the number 10 to the power of 43 (Smith and Morowitz, 1982).

Furthermore, it has been estimated that a metazoan organism may contain and actively use 10,000 to 100,000 different genes (Dawid *et al.*, 1982). Using the lower number, we can calculate the number of possible gene expressions to be 10 to the power of 3000, a number that is totally incomprehensible.

In other words, permutations on the biochemistry and morphology of living substance should, theoretically, be practically infinite but, obviously, this is not the case. Therefore, it would seem that there are regulating factors operating both at the level of the genome and between the genes and their phenotypic expressions that should also be taken into consideration when discussing evolutionary models.

Due to the very nature of their leanings toward teleological evolutionary theory — being steadfastly focussed on natural selection and adaptation — Darwinians generally implicitly, but sometimes explicitly, have come to view evolution as a process guided by extrinsic factors working on randomly generated intrinsic raw-material. However, — as with the

2-3 mm per 1000 years increase in body-height of the horse lineage over 250-300 generations — there are many evolutionary trends observed in the fossil record that have such low rates of morphologic change that from one generation to the other there would have been no change in selective value. Nevertheless, the trends are persistent and therefore must have been driven by intrinsic factors.

Also, if we look at the evolution of organisms as a whole, we find that there is a general trend towards physiologic independence of the environment (i.e. demonstrably developing buffer mechanisms rather than adapting), *viz.* the evolution of osmotic, metabolic and thermal homeostasis (i.e. maintaining a fixed level or value), and behaviour patterns such as hibernation and aestivation (dormancy during periods of drought or heat), and circadian (physiological processes occurring approximately in 24-hour rhythms) and other biorhythms (Maderson *et al.*, 1982).

With regard to the tendency toward a stable body-plan, it has been suggested that this can be interpreted in terms of control theory, *viz.* a regulator develops an internal model of whatever exogenous perturbations that may act on it in order to be homeostatic to those influences. If such a suggestion is true then directional adaptations should arise from intrinsic sources rather than the extrinsic environment (Maderson *et al.*, 1982).

Epigenetic Processes

All of the above discussions suggest the presence of controls acting upon the developing organism. Some of these controls certainly are directly exercised by the regulatory genes, e.g. limiting the number of proteins and body-plans, but there are also other ways of effecting controls on the developing organism. We can collectively refer to these other controls as epigenetic regulatory effects.

Epigenetics deals with those processes that translate the genetic information contained in the newly formed haploid cell into the phenotypic effects observed in the fully developed organism.

These processes may be conveniently grouped into four successively occurring stages of embryogenesis: (1) cell multiplication, (2) cell patterning, (3) cell differentiation and (4) organ morphogenesis.

During the cell multiplication stage the cells are initially totipotent, that is, if separated, they will individually develop into complete organisms. For example, the mouse 8-cell embryo retains this capacity (Saxén and Karkinen-Jaaskelainen, 1981). Shortly thereafter, as the number of cells increases, they lose this capability and become successively more and more "patterned" in preparation for differentiation. What causes this patterning is unknown but it is generally related to their physical position in the developing embryo (Wolpert, 1981). During the cell differentiation

differentiation stage considerable migrations of individual cells and cell groupings takes place; changes in cell morphology also occur at this stage. At this stage only two germ layers, ectoderm and endoderm, are present. However, the third germ layer, the mesoderm, is soon formed through interaction, called induction, between ectoderm and endoderm.

Organ morphogenesis is initially the result of tissue interactions which frequently are sequential and involve different types of tissue and different modes of induction.

All of these processes are guided by epigenetic control systems. The effects of these control systems are mediated by stimuli originating both intrinsically, i.e. from individual cells or cell groupings (tissue), and extrinsically, i.e. from the external environment. The stimuli can be either physical, chemical or mechanical, or combinations thereof. The timing and sequencing of the stimuli resulting in cell patterning, differentiation, and organogenesis are of decisive importance and so also is the fact that these processes appear to follow pathways with feedback loops (Connelley *et al.*, 1981).

Little is known about what exactly these stimuli are, except in general terms, e.g. hormones, enzymes, possible ions, temperature, mechanical forces, etc. How these stimuli are effected at the molecular level is by and large unknown (Wolpert, 1981).

Although the underlying causes for the process called induction are largely unknown, experimental studies have yielded results that are of particular importance for our understanding of evolutionary processes.

Cuticular appendages like scales, feathers and hair originate from interaction between dermis and epidermis. Experiments have shown that the epidermis possesses the actual information for these structures, but that the dermis triggers their initial formation and decides size and distribution. When tissue combinations are done across taxonomic boundaries, the following results are obtained.

With intraclass combinations, e.g. tissue from chick and duck, the appendages develop fully according to the information from the dermis (Figure 2). For example, when epidermis from a feather-bearing area of the chick is combined with dermis from the duck leg, the result is scales. Actually, even epidermis from a glabrous area of the chick produces the same result. If chick epidermis is combined with dermal mesoderm from the mouse, feathers begin to develop, but to reach full development dermal cells from the chick must be added. Experiments involving lizards show similar results. See Saxén and Karkinen-Jaaskelainen (1981) for references.

A spectacular result of interclass induction was obtained by Kollar and Fisher (1980).

They combined pharyngeal epithelium from a chick embryo with dental mesenchyme from a mouse embryo. The result included fully developed teeth, something that the birds have not had since the Cretaceous. In this case, it should also be remembered that teeth have very specialized cells — odontoblasts for dentin and ameloblasts for enamel — and that formation of teeth includes several interactive stages.

In a different type of induction experiment Hampé (1959; see also Alberch *et al.*, 1979) increased the growth rate of the fibula in the chick leg. The resulting fibula, which was larger than normal, came in contact with the metatarsal bones and induced the formation of ankle bones, which are normally lacking in modern birds. These ankle bones were formed in a pattern intermediate between that of the fossil bird *Archaeopteryx* and a reptile (Figure 3).

Certain "sites" in the genome of the developing embryo evidently retain a dormant capacity to produce features thought to have been lost during evolution; the genes are "switched-off" due to altered epigenetic pathways. Spontaneous occurrences of the above type of phylogenetically older expressions are referred to as atavisms. A good example is the occasional occurrence of accelerated growth of the side splints in the horse's foot, which can result in almost fully developed toes.

Systematic studies of this dormant capacity might open up new doors with regard to our understanding of parallel and convergent evolution. "Did the ichthyosaur "dorsal fin" really arise from nothing or might it be (despite its lack of internal structure) the homologue (based on inherited embryological potential) of a fully developed, distant ancestral feature?" (Gould, 1982). The keyword in this quote from Gould is "embryological potential". Certain studies have shown demonstrably that epigenetic pathways may be temporarily "shut down". If we assume for the moment that these pathways are present but dormant, (here we are getting close to the realm of science fiction) then what we have to do is re-activate these pathways in order to recreate some past life forms (would you believe a dinosaur?).

There is accumulating evidence indicating that many inductive processes can be interpreted in terms of mechanical interaction between the cells (Horder, 1981). For example, the initial distribution of cartilage primordia in the head skeleton directly reflects the underlying migration pattern of the neural crest cells and the cells are apparently distributed according to paths of least resistance (Erickson *et al.*, 1980). When the pathways of the crest cells are experimentally modified, the distribution of cartilage primordia follows the new pattern. The folding of the neural tube and its initial anterior expansion and

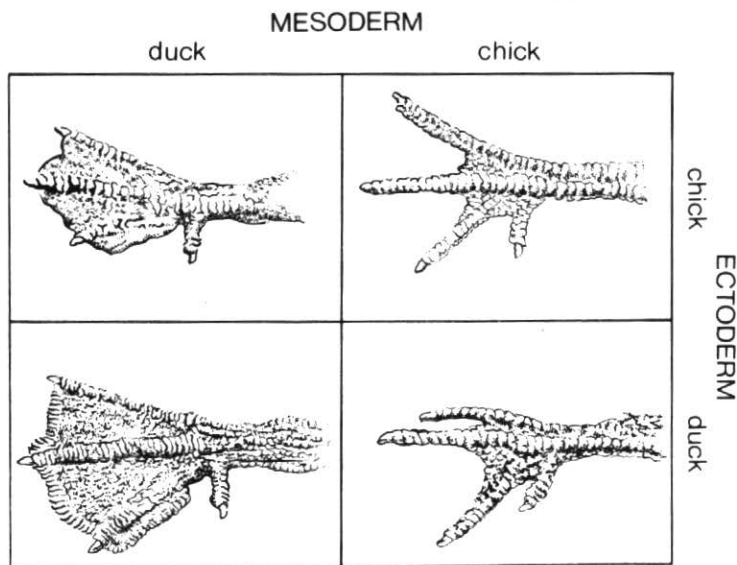


Figure 2 Embryological induction experiment with tissue from duck and chick. When the dermal components are interchanged, the chick foot acquires the characteristic web of the duck foot and the duck foot acquires the morphology of the chick foot; i.e. the dermal component decides. (After Saxén and Karkinen-Jaaskelainen, 1981).

subsequent folding can be explained entirely in terms of mechanical and hydrostatic processes (Jacobsen, 1981). The actual size of the retina in the eye is determined by the pressure of the intraocular fluid (Coulombre, 1956). General morphology and features like processes, grooves and knobs on bones that are involved in movement — like mandible, scapula, long-bones, etc . . . — are the direct result of imposed mechanical stress (see Goss, 1978, for examples and literature). For many more examples of the ubiquity of mechanically explainable morphological features see Horder (1981).

On the other hand, the actual physical size attained by long-bones (Felts, 1959) and vertebrae (Noel and Wright, 1972) and their growth rates are highly autonomous.

The effects of various environmentally induced epigenetic stimuli are readily observed in ecophenotypes. For example, certain cichlid fish acquire a pharyngeal crushing dentition if their diet includes snails with hard shells, but simpler bicuspid piercing teeth if their diet does not include the snails (Greenwood, 1965). Fishes living in unusually warm water have lower numbers of fin rays than those living in waters of more normal temperatures (Kinne, 1964). Other environmentally induced examples are: time of sexual maturation, brood size, body-size and body-form (Rosen and Buth, 1980).

The importance of mechanical stress in the development of skeletal and muscular features is perhaps most dramatically illustrated by Slijper's goat (Figure 4), which was born without fore-limbs. The goat learned to walk on its hind-legs and in the process it developed an S-shaped backbone, modified muscle insertions in the vertebrae, barrel-

shaped chest, broadened sternum, and a broad neck; all features being very strongly correlated with, and considered indices of, bipedalism (Slijper, 1942a, b).

From these examples we can draw at least two conclusions. First, epigenetic processes are highly hierarchically ordered and there must be a continuous feedback system operating in order to keep one developing system in harmony with another. Second, the genome does not, generally, supply a detailed blueprint which is faithfully reproduced by the epigenetic processes, but rather it supplies conceptual plans which are individually realized.

What our increasing knowledge of epigenetic processes teaches us, above all, is that even very minor changes or amplifications of epigenetic stimuli, particularly if applied at an early stage of development, may result in very extensive morphologic and physiologic transformations. In other words, morphologic and physiologic modifications interpreted as being the results of micro- or macro-mutations may in fact be the results of amplified or otherwise slightly altered epigenetic processes. A simple change in timing of development can lead to large-scale modifications of the phenotype.

Heterochrony

Heterochrony refers to shifts in the onset and termination of the timing of somatic and/or sexual development, i.e. the rate of development of an organ or an organ system relative to the rate of development of another organ or organ system (e.g. Gould, 1977a; Alberch *et al.*, 1979).

The most discussed and celebrated type of heterochrony relates to either a speeding-up of sexual development relative to somatic development or a slowing down of the rate of somatic development relative to the rate of sexual development

Both of these processes result in the organism acquiring sexual maturity while retaining certain juvenile features. This condition is generally referred to as being paedomorphic. Paedomorphy includes neoteny, which occurs when somatic development is retarded relative to sexual development, and progenesis, which occurs when sexual development occurs at an earlier than usual stage of development.

A prime example of neoteny is the Mexican axolotl (Figure 5) which does not metamorphose from a larval to an adult stage, as amphibians generally do, but acquires sexual maturity at the larval stage of somatic development. This retardation of otherwise normal development is due to an inhibition of thyroxin production; if fed ground-up thyroids, the axolotl will (partially) metamorphose into a land-living amphibian.

Neoteny, postulated on the basis of allometric growth studies (see below), has recently been considered to be the cause of the origin of the pygmy chimpanzee (*Pan paniscus*) from the "common" chimpanzee (*Pan troglodytes*) (Shea, 1983). More spectacularly, the origin of Man has been suggested by Gould (1977a) to be the outcome of neoteny, and Maderson and co-workers (1982) have recently suggested that the fact that several higher vertebrate taxa generally start out as small-sized inconspicuous organisms should be in favour of a neotenic origin of these vertebrate taxa.

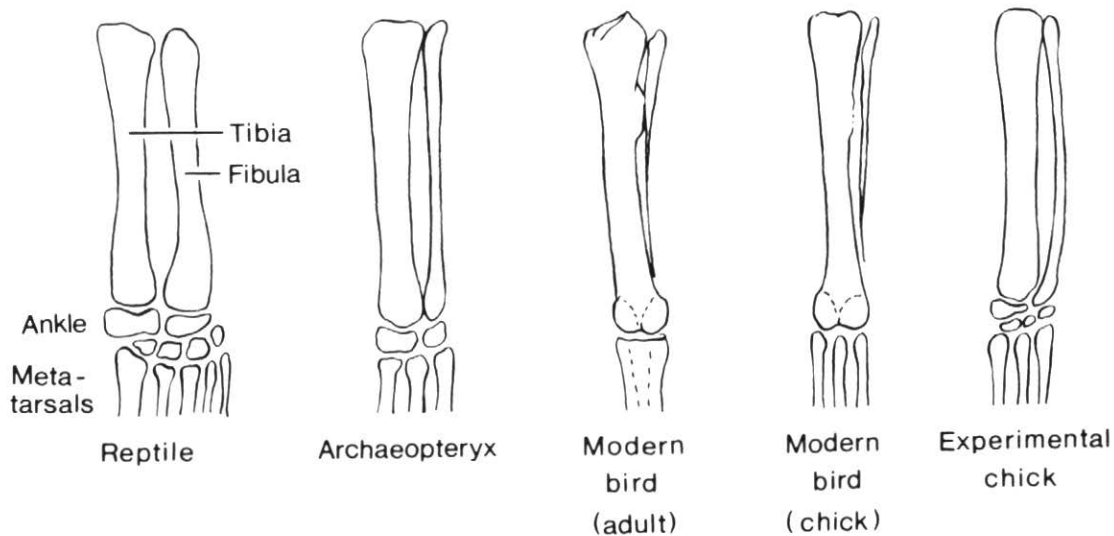


Figure 3 Hampé's (1959) induction experiment. Hampé managed to prolong the growth of the fibula in the chick embryo, thereby causing the induction of ankle bones. Note that modern birds lack ankle bones whereas ankle bones did exist in the Jurassic bird Archaeopteryx and in reptiles. The experimental bird developed ankle bones in a pattern intermediate between that of reptiles and Archaeopteryx. (After Alberch *et al.*, 1979.)

Presently we have no way of estimating how pervasive the processes of neoteny might be in the creation of new taxa. However, on the basis of existing evidence it would seem to be a feasible process, and, as such, certainly should be considered.

Peramorphosis is the result of somatic development continuing beyond the final stage of

development of the ancestor and thus producing new or modified phenotypic expressions (e.g. Gould, 1982). Peramorphosis is well demonstrated in many phylogenetic lineages exhibiting an increase in body-size. The phylogenetic increase in size of the nose-horn in titanotherians (Tertiary mammals) and the progressive increase in growth of the rear-

ward expansion of the head-shield in ceratopsians (Cretaceous dinosaurs) are typical examples of peramorphosis.

Allometry

Allometry refers to rate differences in somatic development of individual parts of the body. For example, until about the fifth month of development the head of a human foetus grows faster than the rest of the body — it grows with positive allometry — thereafter it grows with a slower rate than the rest of the body, i.e. it grows with negative allometry.

This developmental growth relationship is expressed in the empirically derived formula:

$$Y = bX^a$$

where **Y** is a size-related morphologic or physiologic variable, **X** is body weight, **a** is an exponent relating **Y** and **X**, and **b** is a coefficient. Usually, this expression is log-transformed into the form:

$$\log Y = \log b + a(\log X)$$

and its linear expression (regression line) is plotted. This formula has been found to be applicable to a vast number of size-dependent physiologic and morphologic variables; both ontogenetic and phylogenetic, and so-called static "mouse-to-elephant" plots (Figure 6). For introduction to the literature and references, see, as examples, Gould (1966), Gunther (1975), Schmidt-Nielsen (1975), Lindstedt and Calder (1981), Peters (1983), and Calder (1984).

Use of the allometric formula illustrates particularly well the remarkable consistency in scaling (the numerical value of the exponent **a**) that exists between body-size and organ-size, and with physiological processes that occur among organisms varying over several orders of magnitude in size.

For example, the metabolic rate of mammals consistently scales as 3/4 of body size. Brain-weight of mammals also scales with an exponent of 3/4, but frequencies like heart beat, respiratory rate, and other physiological periods, including life-span of mammals and birds, generally seem to be related to the 1/4 power of body weight. Capacities like heart and spleen volume, and respiratory vital capacity all scale isometrically, i.e. close to 1 (for further examples, see Lindstedt and Calder, 1981).

In other words, there are very powerful constraints in the genotype regulating the proportional development of size of organs and the rates of physiological processes.

Reams of literature have been written about morphological and physiological allometries, but only a few have been concerned with evolutionary relationships. For example, the giant Irish "Elk" actually had antlers proportional to its body-size (Gould, 1974); the dinosaurs did not have a smaller relative brain size than other reptiles (Hopson, 1977); and allometric studies have elucidated inquiries into hominid evolution (Pilbeam and Gould, 1974).

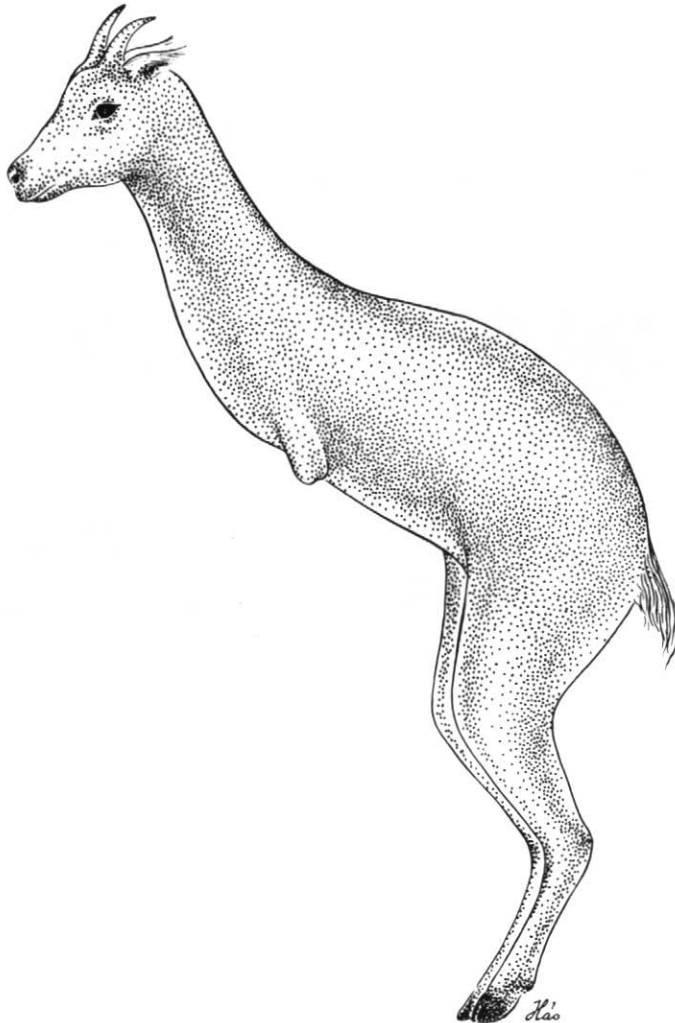


Figure 4 Slijper's goat. The goat was born without fore-limbs but learned to walk on its hind-legs. In the process it developed several anatomical characteristics typical of bipedalism. See text for further explanation.

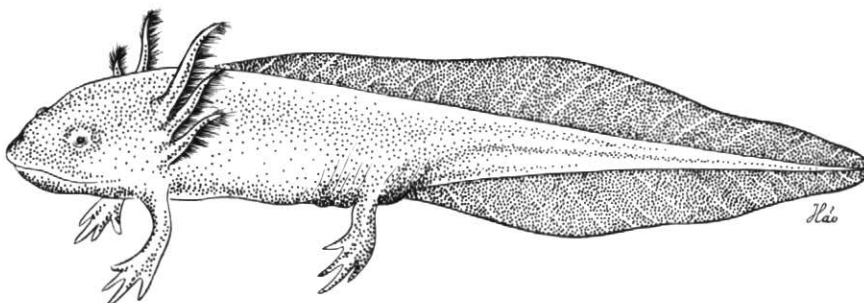


Figure 5 The Mexican axolotl, an example of neoteny. See text for further explanation.

An understanding of allometric principles makes nonsense out of a number of explanations put forward with regard to so-called adaptational features of organisms. For example, if we look at the ridiculously small fore-limbs of the dinosaur *Tyrannosaurus rex* (Figure 7), we will certainly find it difficult to explain them as the result of a gradual adaptation (to what purpose?), but if they are looked upon as the necessary outcome of a phylogenetic increase in body-size coupled with negative allometric growth of the fore-limbs, the problem disappears. Allometric relationships, rather than Lamarckian desires or Darwinian teleology, also apply to the giraffe and its long neck. The giraffe may be supremely adapted to browsing on the upper branches of an African acacia but there is where it ends. Just look at the extremely awkward and vulnerable (i.e. non-adaptive) position (to the attack of lions and other large predators) it has to assume when wanting a drink of water.

If we gain a better understanding of size-correlated modifications of morphological features we do not have to resort to major mutations in order to explain the sometimes rather drastic morphological and physiological alterations that may occur during the evolutionary transition from one taxon to another.

If we couple allometry with heterochrony we have an extremely powerful tool for creating systemic phenotypic modifications with a minimum of genetic input. Consider, for example, the evolutionary transition from insectivore to bat which can be very easily explained in terms of heterochrony affecting allometric growth relationships of the limb bones.

Although interest in allometric relationships has resulted in a vast literature, and even though some authors (e.g. Gould, 1982 and earlier) have pointed out the potential for allometry generating the large-scale morphologic-physiologic gaps observed among living organisms, practically no attempt has been made to incorporate allometric principles on a broad scale in evolutionary theory. The notable exception being Bernhard Rensch (1959) in his now classic text *Evolution above the Species Level* which appeared a quarter of a century ago as a slightly up-dated translation of an earlier German version; in 1972 a further German edition appeared.

Canalization and Entrenchment

Experiments have shown that some alleles exhibiting no phenotypic expression in one environment can cause large-scale modifications in another. These experiments have also demonstrated that continued breeding in the conducive environment may result in genetic "canalization" of the particular phenotypic expression to the extent that if returned to the original environment the new feature will still be expressed (Waddington, 1975); i.e. we should be a little bit more careful when debunking Lamarck.

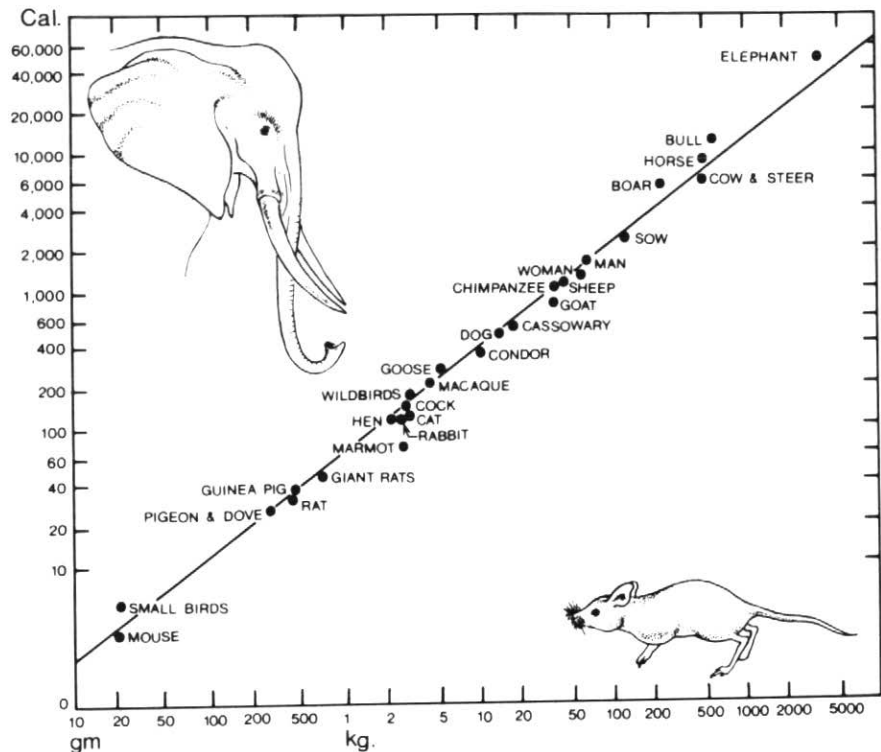


Figure 6 Heat production in birds and mammals related to body weight and plotted logarithmically. Note that even though the size variation spans six orders of magnitude, the adherence to the regression line is very close. This is the so-called "mouse-to-elephant curve". The slope of the line is 0.75. Data points from Benedict, 1938.



Figure 7 *Tyrannosaurus rex*, illustrating negative allometric growth of the fore-limbs coupled with phylogenetic increase in body-size. See text for further explanation.

In this essay I have outlined and discussed a number of mechanisms and processes that can cause large-scale transformations of organisms. How pervasive and phylogenetically stable these transformations are is obviously a function of how deep their genetic bases are "canalized" or entrenched.

The depth of this entrenchment is probably a direct reflection of the degree of redundancy of the particular gene family(-ies) governing the new expressions, i.e. deeply entrenched expressions should be characterized by very high proportions of repetitive DNA buffering against the effects of mutations and novel epigenetic processes. Certain morphologic (and physiologic) expressions are very rigidly fixed, i.e. deeply entrenched, in the genome, whereas others are less deeply entrenched and some are only shallowly entrenched. As examples of the different degrees of entrenchment, we can consider (1) the pervasiveness of the pectoral and pelvic girdles among land-living vertebrates; (2) the frequent departure from pentadactyly among some mammalian groups; and (3) the shape of the bird beak.

In addition to the above examples, we have those expressions that are not yet entrenched but are open to future "canalization". For example, the above-mentioned ecophenotypically plastic expressions, which also include such features as growth-form of trees and latitudinal variation in the pigmentation of the plumage of birds. Slijper's goat also belongs in this category. These latter environmentally and mechanically controlled expressions are generally referred to as adaptations based on the inherent plasticity of the developing phenotype. However, a more explicit explanation would be to say that the developing organism is epigenetically capable of choosing among two or more not yet "canalized" developmental pathways. The argument here is to stress that there is a very pronounced hierarchy with regard to how deeply morphologic and physiologic expressions are entrenched in the genome.

If we agree on the existence of hierarchical entrenchment of gene expressions and that epigenetic systems can be looked upon as buffered control systems with feedback loops, then we would have to assume that an "insult" affecting the genome will be more efficiently buffered the deeper the affected expression is entrenched, and thus less likely to result in an altered phenotypic expression. But if the particular "insult" should happen to establish itself and influence the developmental systems, then we would expect the "snow-balling" effect on the phenotype to increase in direct proportion to increasing depth of entrenchment.

This line of reasoning has some interesting consequences when applied to the observed diversity of extant and fossil organisms. First, it demands a limited number of body-plans; second, it demands the existence of phenotypic gaps systematically increasing in size;

and, third, it demands that the magnitude of these gaps be inversely proportional to their frequency. Empirically, we can show that all three of these consequences are eminently well displayed in our hierarchical classification of organisms and the "hollow curve" obtained when plotting frequency of taxa against taxonomic rank.

Final Words

In a short essay like this it is obviously impossible to present all the arguments that have been raised against such a many-faceted topic as Darwinian Evolution; neither is it possible to do justice to the counter arguments. However, if we consider the phenotypic gaps existing in the living and fossil world of organisms to be truly representative of the course of evolution, then we have to take into account those scientific facts that offer explanations for these gaps.

Micro-evolution occurring at the species level can adequately be explained in terms of natural selection acting on micro-mutations (i.e. point mutations), gene recombinations, genetic drift, etc. That this is so is well evidenced by today's species abundance and the existence of superspecies with their geographic and ecologic variants.

Macro-evolution, on the other hand, occurring above the species level and producing the characteristic phenotypic gaps that can be observed in the living world, has to be credited to processes that can explain these evolutionary saltations. In this essay I have outlined, and argued for, various such processes and mechanisms that have been either experimentally demonstrated or inferred on basis of molecular, embryological, ontogenetic and phylogenetic data.

An acceptance of a dichotomy of evolutionary mechanisms and processes occurring at the species and supra-species levels obviously diminishes the influence and importance of natural selection as a creative force in evolution. However, it certainly has the final say.

Acknowledgements

This essay benefitted greatly from discussions with my wife Dr. Goverdina E. Fähræus-van Ree and a very thorough review by Dr. G.S. Nowlan. The very accomplished art-work was done by Maria Tran T.V.H. Ball.

References

- Alberch, P., Gould, S.J., Oster, G.F and Wake, D.B., 1979, Size and shape in ontogeny and phylogeny: Paleobiology, v. 5, p. 296-317
- Benedict, F.G., 1938, Vital Energetics: A study in Comparative Basal Metabolism: Carnegie Institute of Washington, Washington, D.C., v. 503, 215 p.
- Bernard, B., 1982, ed., Vincent by himself: New York Graphic Society: Little, Brown, and Co., New York, 327 p.
- Bethell, T., 1976, Darwin's mistake: Harpers Magazine, nr. 252, p. 70-75.

- Bonner, J.T., 1982, ed., Evolution and Development: Springer-Verlag, New York, 356 p.
- Brady, R.H., 1979, Natural selection and the criteria by which a theory is judged: Systematic Zoology, v. 28, p. 600-621.
- Britten, R.J., 1982, Genomic Alterations in Evolution, in Bonner, J.T., ed., Evolution and Development: Springer-Verlag, New York, p. 41-64.
- Britten, R.J. and Davidson, E.H., 1969, Gene regulation for higher cells: a theory: Science, v. 165, p. 349-358.
- Burton, N. and Jones, J.S., 1983, Mitochondrial DNA: new clues about evolution: Nature, v. 306, p. 317-318.
- Busch, G.L., 1975, Modes of animal speciation: Annual Review of Ecology and Systematics, v. 6, p. 339-364.
- Calder, A.W., III, 1984, Size, Function, and Life History: Harvard University Press, Cambridge, 431 p.
- Connelley, T.G., Brinkley, L.L. and Carson, B.M., 1982, eds., Genesis and Pattern Formation: Raven Press, New York, 302 p.
- Coulombre, A.J., 1956, The role of introcular pressure in the development of the chick eye. 1. Control of eye size: Journal of Experimental Zoology, v. 133, p. 211-225.
- Darwin, C., 1859, On the Origin of Species by means of Natural Selection. (reprint of second edition): Oxford University Press, 454 p.
- Davidson, E.H., 1982, Evolutionary change in genomic regulatory organization: Speculations on the origins of novel biological structure, in Bonner, J.T., ed., Evolution and Development: Springer-Verlag, New York, p. 65-84.
- Dawid J., et al., 1982, Genomic change and morphological evolution, in Bonner, J.T., ed., Evolution and Development: Springer-Verlag, New York, p. 19-39.
- Dover, G.A., 1980, Ignorant DNA?: Nature, v. 285, p. 618-620.
- Dover, G.A., Strachan, T. and Brown, S.D.M., 1981, The Evolution of genomes in Closely-related Species, in Scudder, G.G.E. and Reveal, J.L., eds., Evolution Today, Proceedings of the Second International Congress of Systematic and Evolutionary Biology: Hunt Institute for Botanical Documentation, Carnegie-Mellon University, Pittsburgh, Pennsylvania, p. 337-350.
- Eldredge, N. and Gould, S.J., 1972, Punctuated equilibria: an alternative to phyletic gradualism, in Schopf, T.J.M., ed., Models in Paleobiology: Freeman, Cooper and Company, San Francisco, p. 82-115.
- Enckson, C.A., Tosney, K.W. and Weston, J.A., 1980, Analysis of migratory behavior of neural crest and fibroblastic cells in embryonic tissues: Developmental Biology, v. 77, p. 142-156.
- Fähræus, L.E., 1982, Allopatric speciation and lineage zonation exemplified by the *Pygodus serrus* - *P. anserinus* transition (Conodontophorida, Ordovician): Newsletter of Stratigraphy, v. 11, p. 1-7.
- Felts, W.J.L., 1959, Transplantation studies of factors in skeletal organogenesis. 1. The subcutaneously implanted long-bone of the rat and mouse: American Journal of Physical Anthropology, v. 17, p. 201-215.
- Frazzetta, T.H., 1970, From hopeful monster to bolyerine snakes?: American Naturalist, v. 104, p. 55-72.

- Goldschmidt, R., 1940, *The Material Basis of Evolution*: Yale University Press, New Haven, Connecticut, 436 p.
- Goss, R.J., 1978, *The Physiology of Growth*: Academic Press, New York, 441 p.
- Gould, S.J., 1966, Allometry and size in ontogeny and phylogeny: *Biological Review*, v. 41, p. 587-640.
- Gould, S.J., 1974, The evolutionary significance of "bizarre" structures: antler size and skull size in the "Irish Elk", *Megaloceros giganteus*: *Evolution*, v. 28, p. 191-220.
- Gould, S.J., 1976, Darwin's untimely burial: *Natural History*, v. 85, p. 24-30.
- Gould, S.J., 1977a, *Ontogeny and Phylogeny*: Harvard University Press, Cambridge, Massachusetts, 501 p.
- Gould, S.J., 1977b, The return of hopeful monsters: *Natural History*, v. 86, p. 22-30.
- Gould, S.J., 1982, Change in developmental timing as a mechanism of macro-evolution. *in* Bonner, J.T., ed., *Evolution and Development*: Dahlem Konferenzen, Springer-Verlag, Berlin, p. 333-346.
- Greenwood, P.H., 1965, Environmental effects on the pharyngeal mill of cichlid fish, *Astatoreochromis alluandi*, and their taxonomic implications: *Proceedings of the Linnean Society of London*, v. 176, p. 1-10.
- Gunther, B., 1975, Dimensional Analysis and the Theory of Biological Similarity: *Physiological Review*, v. 55, p. 659-699.
- Hampé, A., 1959, Contribution à l'étude du développement et de la régulation des déficiences et des excédents dans la patte de l'embryon de poulet: *Archives Anatomique de Microscopie Morphologie Experimentelle*, v. 48, p. 345-478.
- Hopson, J.A., 1977, Relative brain size and behavior in Archosaurian reptiles: *Annual Review of Ecology and Systematics*, v. 8, p. 429-448.
- Order, T.J., 1981, Or not throwing the Baby out with the Bath Water, *in* Scudder, G.G.E. and Reveal, J.L., eds., *Evolution Today*. *Proceedings of the Second International Congress of Systematic and Evolutionary Biology*: Hunt Institute for Botanical Documentation, Carnegie-Mellon University, Pittsburgh, Pennsylvania, p. 163-180.
- Jacob, F., 1977, Evolution and tinkering: *Science*, v. 196, p. 1161-1166.
- Jacobsen, A.G., 1981, Morphogenesis of the Neural Plate and Tube, *in* Connelley, T.G., Brinkley, L.L. and Carson, B.M., eds., *Genesis and Pattern Formation*: Raven Press, New York, p. 233-264.
- Kinne, O., 1964, Non-genetic adaptation to temperature and salinity: *Helgoland Wissenschaftliche Meeresuntersuchungen*, v. 9, p. 433-458.
- King, A.S. and McLelland, J., 1979, ed., *Form and Function in Birds*, v. 1, 459 p.
- Kollar, E.J. and Fisher, C., 1980, Tooth induction in chick epithelium: Expression of quiescent genes for enamel synthesis: *Science*, v. 207, p. 993-995.
- Lindstedt, S.L. and Calder, W.A., III, 1981, Body Size, physiological time, and longevity of homeothermic animals: *The Quarterly Review of Biology*, v. 56, p. 1-16.
- Maderson, P.F.A., and many others, 1982, The role of Development in Macroevolutionary Change, *in* Bonner, J.T., ed., *Evolution and Development*: Springer-Verlag, New York, p. 279-312.
- Maynard Smith, J., 1978, Optimization theory in evolution: *Annual Review of Ecology and Systematics*, v. 9, p. 31-56.
- Noel, J.F. and Wright, E.A., 1972, The growth of transplanted mouse vertebrae; effects of transplantation under the renal capsule, and the relationship between the rate of growth of the transplant and the age of the host: *Journal of Embryology and Experimental Morphology*, v. 28, p. 633-645.
- Peters, R.H., 1976, Tautology in evolution and ecology: *American Naturalist*, v. 10, p. 1-12.
- Peters, R.H., 1983, *The ecological implications of body size*: Cambridge University Press, Cambridge, United Kingdom, 329 p.
- Pilbeam, D. and Gould, S.J., 1974, Size and scaling in human evolution: *Science*, v. 186, p. 892-901.
- Rensch B., 1959, *Evolution above the Species Level*: Methuen and Co. Ltd., London, 419 p.
- Rensch B., 1972, *Neuere Probleme der Abstammungslehre. Die Transspezifische Evolution*, Third Edition: Enke, Stuttgart, 468 p.
- Rosen, D.E. and Buth, D.G., 1980, Empirical evolutionary research versus neo-Darwinian speculation: *Systematic Zoology*, v. 29, p. 300-308.
- Saxén, L. and Karkinen-Jaaskelainen, M., 1981, Biology and Pathology of Embryonic Induction, *in* Connelley, T.G., Brinkley, L.L. and Carson, B.M., eds., *Genesis and Pattern Formation*: Raven Press, New York, p. 21-48.
- Schindewolf, O., 1936, *Paläontologie, Entwicklungslehre und Genetik*: Borntraeger, Berlin, 506 p.
- Schmidt-Nielsen, K., 1975, Scaling in Biology: The consequences of size: *The Journal of Experimental Zoology*, v. 194, p. 287-308.
- Scudder, G.G.E. and Reveal, J.L., 1981, eds., *Evolution Today*. *Proceedings of the Second International Congress of Systematic and Evolutionary Biology*: Hunt Institute for Botanical Documentation, Carnegie-Mellon University, Pittsburgh, Pennsylvania, 485 p.
- Shea, B.T., 1983, Paedomorphosis and Neoteny in the Pygmy Chimpanzee: *Science*, v. 222, p. 521-522.
- Slijper, E.J., 1942a, Biologic-anatomical investigations on the bipedal gait and upright posture in mammals, with special reference to a little goat, born without fore-legs. I.: *Proceedings Koninklijk Nederlandse Akademie Wetenschappen*, v. 45, p. 288-295.
- Slijper, E.J., 1942b, Biologic-anatomical investigations on the bipedal gait and upright posture in mammals, with special reference to a little goat, born without fore-legs. II.: *Proceedings Koninklijk Nederlandse Akademie Wetenschappen*, v. 45, p. 407-415.
- Smith, T.F. and Morowitz, J.J., 1982, Between history and physics: *Journal of Molecular Evolution*, v. 18, p. 265-282.
- Stanley, S.M., 1979, *Macroevolution, Pattern and Process*: W.H. Freeman and Company, San Francisco, 332 p.
- van Steenis, C.G.J., 1969, Plant speciation in Malesia, with special reference to the theory of non-adaptive saltatory evolution: *Biological Journal, Linnean Society of London*, v. 1, p. 97-133.
- Waddington, C.H., 1975, *The evolution of an evolutionist*: Cornell University Press, Ithaca, New York, 328 p.
- White, M.J.D., 1978, *Modes of Speciation*: W.H. Freeman and Company, San Francisco, 455 p.
- Wolpert, L., 1981, Positional Information, Pattern Formation, and Morphogenesis, *in* Connelley, T.G., Brinkley, L.L. and Carson, B.M., eds., *Genesis and Pattern Formation*: Raven Press, New York, p. 5-20.

Accepted, as revised, 15 June 1986.