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AN EVOLUTIONARY MANIFESTO: A NEW HYPOTHESIS FOR ORGANIC CHANGE

by John A. Davison, Ph.D.

THIS TREATISE IS DEDICATED TO THE MEMORY OF SIX GREAT SCIENTISTS

William Bateson
Leo S. Berg
Robert Broom
Richard B. Goldschmidt
Pierre Grassé
Otto Schindewolf

> *A dwarf standing on the shoulders of a giant*
> *may see farther than a giant himself.* –
> Robert Burton

> *No sadder proof can be given by a man of his own*
> *littleness than disbelief in great men.* –
> Thomas Carlyle

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PREFACE

This work represents an elaboration of material presented by the author in courses offered here at the University of Vermont, especially Biology 255, The Comparative Physiology of Reproduction and Biology 202, Quantitative Biology. It is my hope that this treatise will reach not only the professional biologist but all others who realize how little we really understand concerning the history of life on this planet. I have assumed little in the way of background and I have defined most technical terms as they appear. The basic ideas put forth here were first published in 1984. I hope that this expanded and more completely documented treatment will reach a larger and more receptive audience.

My own background is in General and Developmental Physiology which is to say that I am interested in how things work. Like others before me, I have come to the realization that Darwinism simply does not work. That conclusion has led to a series of questions which I pose and attempt to answer. Answering one question often leads to asking another. Only by asking questions is one compelled to provide answers. I employ that approach throughout this presentation.

Among those questions are the following: Is evolution finished? Is sexual reproduction incapable of supporting evolutionary change? Is selection, natural or artificial, incapable of producing new lifeforms? In contrast to the Darwinian view, has evolution proceeded by means of leaps (saltation) rather than gradually through intermediate forms? Is there an alternative to Darwinism which, unlike that hypothesis, is compatible with all the facts revealed by paleontology, embryology, cytology, taxonomy, physiology and genetics? Do internal factors have a role in evolution? Is evolution irreversible? Is the individual, rather than the population, the instrument of evolutionarychange? Are there laws governing evolution? Is there compelling evidence that evolution (phylogeny), like the development of the individual (ontogeny), involves the release or derepression of preformed information?

Finally, the most controversial question of all: Has evolution been guided?

With the exception of the last question, to which no certain answer will probably ever be given, I will answer yes to each of these questions. I realize these claims will seem outrageous to the doctrinaire Darwinian. I can only explain that I have not arrived easily at these convictions but have been driven to them through a host of incontrovertible realities that demand those responses. I ask only that the evidence be heard. I cannot overemphasize the debt that I owe to my many predecessors, especially those six to whom I dedicate this work. Their monumental contributions speak for themselves and they should be given serious consideration by every thinking person. Without them I would have been unable to proceed. Whenever possible, I quote them directly so there can be no misunderstanding about what they meant. Most of the quotations from authors not in the cited literature are from the sixteenth edition of *Bartlett's Familiar Quotations*.

I owe a very special debt to Dr. Judith Van Houten, Chair of the Department of Biology and Associate Dean of the College of Arts and Sciences. In addition to freezing my salary, her continuing and largely successful attempts to isolate me from the students have served only to provide me with a powerful incentive to continue the search for the truth concerning the great mystery of Evolution. We are once more reminded of the profound significance of Arnold Toynbee's celebrated aphorism:

The Virtues of Adversity

I. Introduction

New opinions are always suspected and usually opposed, without any great reason but because they are not already common. -- John Locke *The decisive step in evolution, the first step toward macroevolution, the step from one species to another, requires another evolutionary method than that of sheer accumulation of micromutations*. -- Richard B. Goldschmidt

I begin with the very last words in Darwin's *Origin of Species*: ... endless forms most beautiful and most wonderful have been, and are being, evolved. I will show that the last three words are without foundation for the vast majority of higher life forms, both those which have existed in the past as well as those which are still extant today. I am aware of the effect of such an assertion and I am delighted to accept the responsibility of demonstrating its validity.

Several years ago, when I was still teaching introductory biology, a rumor got started among the students that I didn't believe in evolution. I finally responded in lecture by indicating that the rumor was entirely correct.

I told the students that I did not "believe" in evolution; *I knew that it had occurred*. I hoped by this means to impress upon the students the difference between matters of belief (faith) and matters of knowledge.

Darwinism is a matter simply of belief since the progressive evolution of no creature now living has ever been demonstrated. As an experimentalist I am not impressed by unconfirmed hypotheses and accordingly I began casting about for possible explanations for this remarkable state of affairs. Accepting the reality that evolution has occurred leads to the question as to whether or not it is still occurring and, if not, why not? I will present a substantial body of evidence indicating that the evolution of higher organisms is at a virtual standstill, a conclusion that had been reached by others long before me.

Let me take this opportunity to acknowledge the huge debt that we all owe to some of the greatest biologists of the twentieth century. Among them are the Russian ichthyologist and zoogeographer Leo S. Berg (1876-1950), the geneticists Richard B. Goldschmidt (1878-1958) and William Bateson (1861-1926), the paleontologists Otto Schindewolf(1896-1971) and Robert Broom (1866-1951) and the French zoologist Pierre Grassé (1895-1985). Each is a widely acclaimed scholar of the first rank and not one could be described as an armchair theoretician. They had each disclosed major difficulties with the Darwinian model and had discussed them at great length in their books and papers. I am very pleased to be able to consolidate and incorporate many oftheir common and often independent conclusions into a new hypothesis of organic evolution. This is a truly international assemblage of investigators with Otto Schindewolf coming from Germany, Robert Broom from Scotland and later South Africa, Leo Berg from Russia, Pierre Grassé from France, William Bateson from England and Richard Goldschmidt, a naturalized American who escaped Nazi Germany. All the more remarkable then is the unity of their perspectiveson the complete failure of the Darwinian hypothesis. By way of contrast, Ernst Mayr, in his *opus magnus*, *The Growth of Biological Thought* (1982), deals with these six skeptics as follows. Broom is not even mentioned. The books by Grassé (1973) and Berg (1969) are listed in the bibliography, but no reference to either author is made in the text. Goldschmidt and Schindewolf are dispensed with in a few words. Only Bateson is given a remotely even-handed treatment. Perhaps it is understandable why Mayr short changed these scientists since on page 132 he made his position indelibly plain (literally) by describing himself as a "dyed-in-the-wool Darwinian"!

The new mechanism, which I have called *the semi-meiotic hypothesis*, is based upon an obvious fact that has been before us for a very longtime. It has to do with the manner in which the sex cells, the eggs and sperm, are formed. This process, known as meiosis or chromosomereduction, occurs in two steps. Prior to the first meiotic division the chromosomes become duplicated as they do in mitosis. Then two divisions take place. The first returns the chromosome number tothe diploid state and so can be considered to be a form of diploid presexual reproduction. This first division takes place in a special way which I feel provides the mechanism of macroevolution. Also since the second division cannot occur until the first has taken place, the first meiotic division is logically the more primitive of the two and accordingly must have evolved first (Davison 1984 1993 1998). Upon this premise I proceed.

II. Is evolution finished?

All intelligent thoughts have already been thought; what is necessary is only to try to think them again. – Goethe *It is undesirable to believe a proposition when thereis no ground whatsoever for supposing it to be true.* -- Bertrand Russell

II-1. Why has Darwinism prevailed?

Darwinism has prevailed entirely for negative reasons since alternative hypotheses have proven to be inadequate. Chief amongthese is Lamarckism or the genetic transmission of characters acquired during the life of the individual. Such transmissions have never been demonstrated at least in higher forms. Accordingly, in the absence of experimental verification, Lamarckism cannot be given serious consideration. A second alternative view is Creationism. Here caution must be observed. While it is true that the existence of a Creator, whilea logical necessity, has never been rigorously proved and perhapsnever can be, it is also true that neither has been the spontaneous generation of life. Pasteur's flasks, on display at the Sorbonne and open to the air, remain sterile to this day and there is no evidence whatsoever from the geological record to support the celebrated "organic soup" hypothesis for spontaneous generation. Perhaps the most compelling feature for the Darwinists resides intheir persistent conviction that all of evolution is the result of blind chance. In so doing, the Darwinists refuse to consider that evolution might be subject to laws and precise mathematical relationships such as those that govern virtually every aspect ofthe inanimate world. Obvious examples are Galileo's Law of Falling Bodies, Newton's Laws of Motion and Einstein's equation of energy and mass. One must be prepared to realize that there may be comparable laws at work in the living world. Furthermore, blind chance demands that life should have arisen and should still be arising on countless other planets in the vast cosmos, yet there is no evidence that life exists now, or has ever existed anywhere, except on this planet. With all our advanced technology, we still have not been able to produce even the simplest organic system which could even remotely be described as being alive. Are we to believe that mere chance can accomplish that which has proven quite impossible for the enlightened scientist to achieve? I regard that notion as absurd! I quote Albert Einstein on the matter of chance: "I shall never believe that God plays dice with the world. "If Einstein's physical world does not operate through chance, would one really expect the living world to do so? I, as others before me, do not think so. The Darwinists' stubborn refusal to consider any possible role for laws, order and purpose is what primarily accounts for their failure to present a rational mechanism for evolutionary change. Technically, Darwinism is not even a theory. It is only a hypothesis which, to this day, remains totally devoid of experimental and descriptive verification. Theories, *sensu strictu*, are hypotheses which, having been tested, have been found valid. For example, Einstein's Special Theory of Relativity remained a hypothesis until it had been verified. Only then did it become a theory. Scientists, after all, are expected to maintain open minds. But do they? Sadly, I must answer that question -- Not always!

II-2. Living and nonliving systems compared

One of the most influential of Darwin's predecessors was the geologist Charles Lyell. He expounded the concept of uniformitarianism. Stated simply, he believed that the forces we now see gradually reshaping the surface of the earth have operated the same way throughout the past. This idea gave Darwin the necessary timescale to account for the gradual evolution of the life forms we now see. His total acceptance of the uniformitarian doctrine is clearly evident in those closing words of the *Origin* which I quoted in the introduction: "*... have been, and are being,* *evolved*". Can the notion of uniformitarianism be applied to living systems? The answer at every level is a resounding no. A muscle cell, having contracted, must relax before it can contract again. An amoeba grows and then it stops to divide before it recommences growth. Embryos undergo cellular differentiation, then stop when the definitive state is reached. Most creatures grow until they reach adult size and then stop. In other words, living systems practice autoregulation and self-limitation. These are fundamental distinctions between the animate and inanimate worlds (Davison 1998). I now present the evidence that evolution, like other biological processes, has also been subject to autoregulation.

II-3. The evidence from paleontology

The question -- Is evolution finished? -- like all others concerning evolution, must ultimately be reconciled with the fossil record. I have no credentials as a paleontologist, so I will offer the views of two authorities, the first a professed Darwinian and the second a skeptic of Darwinism. Julian Huxley, the grandson of Thomas Henry Huxley, published what unfortunately proved to be an excessively influential book in 1942. *Evolution: The Modern Synthesis* summarized a consensus among certain geneticists, systematists and paleontologists that evolution was a Darwinian phenomenon, guided by chance and natural selection. Among these were the geneticist Theodosius Dobzhansky, the ornithologist Ernst Mayr and the paleontologist George Gaylord Simpson. Perhaps the most remarkable feature of the text is the revealing and totally contradictory summary that Huxley offers on page 571, seven pages from the end. Evolution is thus seen as a series of blind alleys. Some are extremely short -- those leading to new genera and species that either remain stable or become extinct. Others are longer -- the lines of adaptive isolation within a group such as a class or subclass, which run for tens of millions of years before coming up against their terminal blank wall. Others are still longer -- the links that in the past led to the development of the major phyla and their highest representatives; their course is to be reckoned not in tens but in hundreds of millions of years. But all in the long run have terminated blindly. That of the echinoderms, for instance, reached its climax before the end of the Mesozoic. For arthropods, represented by their highest group, the insects, the full stop seems to have come in the early Cenozoic. Even the ants and bees have made no advance since the Oligocene. For the birds, the Miocene marked the end; for the mammals the Pliocene. Note Huxley's language: *blind alley, terminal blank wall, terminated blindly, full stop* and *marked the end*. Is this language compatible with the Darwinian perspective? Of course it isn't! Robert Broom, who was certainly no Darwinian, had reached comparable conclusions: There is, however, no doubt that evolution, so far as new groups are concerned, is at an end. That a small line of generalized animals should have continued on till in Eocene times the Primates originated and then ceased, and that except for specializations of Eocene types there has been no evolution in the last forty million years, and that the evolutionary clock has so completely run down that it is very doubtful if a single new genus has appeared on earth in the last two million years ... *The Coming of Man* (1933) In Eocene times -- say between 50,000,000 and 30,000,000 years ago -- small primitive mammals rather suddenly gave rise to over a dozen very different Orders -- hoofed animals, odd-toed and even-toed, elephants, carnivores, whales, rodents, bats and monkeys. And after this there were no more Orders of mammals ever evolved. There were great varieties of evolution in the Orders that had appeared, but strangely enough Nature seemed incapable of forming any more new Orders. What is equally remarkable, no new types of birds appear to have evolved in the last 30,000,000 years. And most remarkable of all, no new family of plants appears to have evolved since the Eocene. All major evolution has apparently come to an end. No new types of fishes, no groups of molluscs, or worms or starfishes, no new groups even of insects, appear to have been evolved in these latter 30,000,000 years. *Finding the Missing Link* (1951), page 107 Only once -- perhaps in Cambrian times -- did an invertebrate give rise to a vertebrate, and the invertebrate ancestor seems to have early become extinct. And today, there is no invertebrate that could again give rise to a vertebrate. "Evolution as the paleontologist sees it" (1932), page 68 There are no mammals today in the world that are not already specialized so far that they can never evolve into anything very different. Ibid., page 69 In a demonstration of his faith, Broom continued: As evolution has practically finished and cannot be repeated unless all higher life is wiped off the earth and a new start made from the very beginning, we may perhaps conclude that man is the end to which some power has guided evolution. Ibid., page 71 I discovered that Broom and Huxley had corresponded on this matter as early as 1933 as revealed by the following: And a few zoologists are beginning to recognize that evolution is slowing down, if not quite stopped.

In a letter I had from Professor Julian Huxley only a few months ago he says, "I have often thought about your idea of the fading out of evolutionary potency, and though I cannot pretend to agree with some of the philosophical corollaries which you draw from it, I more and more believe that it is of great importance as a fact." "Evolution -- Is there intelligence Behind It?" (1933), page 14 While Huxley shared Broom's scientific conclusions, it is not surprising that as a humanist (as opposed to a deist) he did not agree that evolution may have been guided. Nevertheless, one might ask -- If it has not been guided, then why has it stopped? I address the question of guidance in a later section. Without mentioning either Huxley or Broom, the French zoologist Pierre Grassé reached the same conclusion. Curiously, the following comments by Grassé (with which I agree completely) stand in marked contrast to the title of the book which is their source! Facts are facts; no new broad organizational plan has appeared for several hundred million years, and for an equally long time numerous species, animal as well as plant, have ceased evolving. ... At best, present evolutionary phenomena are simply slight changes of genotypes within populations, or substitution of an allele with a new one. *Evolution of Living Organisms* (1977), page 84 In order to proceed I am going to accept the consensus of Huxley, Broom and Grassé that evolution has indeed ceased, at least for the majority of higher life forms. Thus, intrinsic to the evolutionary process itself has been the capacity to bring it to a halt, thereby demonstrating auto regulation. One might now ask -- Is it possible to observe, and thereby explain, a mechanism that is no longer in operation? To this question I answer -- Of course not, which means that one must attempt to reconstruct that mechanism from contemporary observations. That reconstructive synthesis is a primary goal of this treatise. Another feature of evolutionary history bears on the question of autoregulation. The vast majority of all the organisms that ever existed have become extinct. I propose that they became extinct *because they could no longer evolve* or otherwise manage to survive. Isn't it interesting that today we see rampant extinction, and the list of endangered species continues to grow, yet no one has observed the progressive evolution of any one of these forms as a response to the challenges offered by a changing environment. Admittedly, man is altering the environment at an unprecedented rate. Aren't these precisely the conditions that should be evoking dramatic evolutionary responses? Where are they?

II-4. Sexual and asexual reproduction compared

While sexual reproduction is characteristic of most higher plants and animals, it is by no means universal. Many plants and animals do not practice sex and reproduce exclusively asexually. Every phylum in both the animal and plant kingdoms has representatives that reproduce asexually or, as it is also described, parthenogenetically orgynogenetically. In the majority of these cases parthenogenesis isessentially mitotic with the offspring being genetic replicas (clones) of the parent. Why is this very conservative form of reproduction so commonplace? Here is one suggestion. Sexual reproduction involvesthe segregation and recombination of those genes contained in the two parental organisms. Frequently the new combinations prove to be inferior to those of the parents. Clonal (mitotic) parthenogenesis precludes this possibility. Such creatures have no known means of genetic recombination and accordingly would seem incapable of adapting to a changing environment, yet many of them have been eminently successful, enduring unchanged perhaps even for millions of years. Why change the genome if it has already successfully established its capacity to grow and reproduce? The single-celled *Amoeba* presents an interesting example. This animal manages famously. As long as it can reproduce faster than it acquires deleterious mutations it can survive indefinitely and unchanged. The same can be said for many other life forms in both the plant and animal kingdoms and of course for the prokaryotes (bacteria and blue-green algae) as well. The evidence that evolution may be finished coupled with the fact that so many organisms reproduce sexually raises a provocative question --can sexual forms evolve? Before I supply an answer to that question, here are some relevant observations.

II-5. The failure of selection

[Selection] cannot, therefore, be an agency for the production of new forms. -- Leo S. Berg *[Selection] acts more to conserve the inheritance of the species than to transform it*. -- Pierre Grassé Man has practiced intensive selection for centuries, yet has failed to produce new species by this means. Most parthenogenetic forms offer little or nothing to select and so nearly all of man's efforts have been with creatures which reproduce sexually. Dogs present an instructive example. In addition to the many working breeds, man has produced some bizarre creatures like the Chihuahua and the Dachshund as well as giant animals like the Great Dane,

the Mastiff and the Saint Bernard. Great variations in color, coat quality and even temperament have also been produced. These differences are due to the action of Mendelian genes segregating and recombining in sexual reproduction. The result is that the products are able to interbreed not only with each other but with the wolf as well. The hybrids are fertile which is to say that they are not physiological hybrids at all, indicating that no real evolution has taken place. It should also be noted that selection, when carried to the extreme, invariably results in a loss of fitness as is so obvious for example in the shortened life spans of the Saint Bernard, the Great Dane and the English Bulldog. The Danish biologist Ojvind Winge described an interesting test of speciation in his book *Inheritance in Dogs*. A male Saint Bernard spontaneously mated with a female Dachshund which subsequently delivered a litter. One member of this litter became pregnant and delivered a normal litter herself proving that no real speciation had occurred during the long period of separation of the parental breeds. This female had, however, inherited her large body from the Saint Bernard sire but the short legs from the Dachshund bitch with the result that her belly dragged on the ground during her pregnancy and had to be protected with towels! (Winge 1950, page 44.) An even more impressive example of the failure of selection is offered by the goldfish. Starting with the Asiatic carp *Carassiusauratus*, the Chinese and Japanese have derived some strange creatures such as those with telescopic eyes some of which even gaze upward as in the variety "celestial". They have even produced forms which depart from the fundamental vertebrate character of possessing two pairs of lateral appendages, the pectoral and pelvic fins, corresponding to our arms and legs respectively. By duplicating the anal fin they converted the fish to a potential hexapod! They also duplicated the caudal fin, a condition unknown in the natural world and even suppressed the dorsal fin, a basic character in virtually all fishes. The variety "celestial" combines all of these features and is blind as well. None of this has produced any semblance of speciation and the animals are still Asiatic carp. Why do these attempts fail? Apparently they fail because they represent the selection for individual mutant genes, from which one can draw the formal conclusion that such alterations may have little or nothing to do with the evolutionary process. It should also be noted that dogs and goldfish reproduce only by sexual means. In his remarkable book *Nomogenesis; or, Evolution Determined by Law* (Russian edition 1922, English edition 1969) Leo Berg quotes the American paleontologist Henry Fairfield Osborn on selection: In all the research since 1869 on the transformations observed in closely successive phyletic series no evidence whatever, to my knowledge, has been brought forth by any paleontologist, either of the vertebrated or invertebrated animals, that the fit originates by selection from the fortuitous. Osborn, quoted in *Nomogenesis* (1969), page 127 In the same volume, on page 314, Berg cites R.C. Punnett, who originated the familiar Punnett square for the solution of problems in Mendelian segregation and recombination. From Punnett's book on mimicry: Natural selection is a real factor in connection with mimicry, but its function is to conserve and render preponderant an already existing likeness, not to build up that likeness through the accumulation of small variations, as is so generally assumed. *Mimicry in Butterflies* (1915), page 152 Berg's own views are expressed as follows: An organism is a stable system, in which a tendency toward variation is confined within certain limits by inheritance. This truth is self evident. It would be impossible to conceive how such complex organs as the eye, the ear or the pituitary body could properly exercise their functions, if they were the seat of an infinite number of variations, from which it would be left to chance to select the most efficient. *Nomogenesis*, page 27. The laws of the organic world are the same, whether we are dealing with the development of an individual (ontogeny) or that of a paleontological series (phylogeny). Neither in the one nor in the other is there room for chance. Ibid., page 134. William Bateson had offered, even before 1900, a similar appraisal of selection: For the crude belief that living beings are plastic conglomerates of miscellaneous attributes, and that order of form or Symmetry have been impressed upon this medley by Selection alone; and that by Variation any of these attributes may be subtracted or any other attribute added in indefinite proportions, is a fancy which the Study of Variation does not support. *Materials for the Study of Variation* (1894), page 80. The many converging lines of evidence point so clearly to the central fact of the origin of the forms of life by an evolutionary process that we are compelled to accept this deduction, but as to almost all the essential features, whether of cause or mode, by which specific diversity has become what we perceive it to be, we have to confess an ignorance nearly total. The transformation of masses of population by imperceptible steps guided by selection, is, as most of us now see, so inapplicable to the facts, whether of variation or of specificity, that we can only marvel both at the want of penetration displayed by the advocates of such a proposition, and at the forensic skill by which it was made to appear acceptable even for a time. *Problems of Genetics* (1913), page 248.

And it is apparently still considered to be acceptable by the majority of evolutionary biologists. I am quite unable to understand how that can be. I agree with all of the foregoing by concluding that the primary effect of natural selection is to prevent change. In so doing, I do not challenge the reality of natural selection; I merely point to its transparent failure as a progressive evolutionary device. On the other hand, one must accept the fact that it is Nature that ultimately does the selecting. Since new life forms have obviously been allowed to persist, at least for a while, the question becomes simply -- How have new forms been produced, sexually or by someother means? This consideration leads to the next question.

II-6. Can sexual forms evolve?

Nothing is so firmly believed as what is least known. – Montaigne I am by no means the first to question the capacity of sexual reproduction to support significant evolutionary change. The horticulturist Luther Burbank was not an academician; he claimed to have received his education at the University of Nature. From his autobiography: There is a law of which I have not yet spoken that is useful to plant-breeders, as well as being a limitation on them. It is called the "Law of the Reversion to the Average". I know from my experience that I can develop a plum half an inch long or one two and a half inches long, with every possible length in between, but I am willing to admit that it is hopeless to try to get a plum the size of a small pea, or one as big as a grapefruit. I have daisies on my farm little larger than my finger nail and some that measure six inches across, but I have none as big as a sunflower, and never expect to have. I have roses that bloom pretty steadily for six months in the year, but I have none that will bloom twelve, and I will not have. In short, there are limits to the developments possible, and these limits follow a law. But what law, and why? It is the law that I have referred to above. Experiments carried on extensively have given us scientific proof of what we had already guessed at by observation; namely, that plants and animals all tend to revert, in successive generations, toward a given mean or average. Men grow to be seven feet tall, and over, but never to ten; there are dwarfs not higher than 24 inches, but none that you can carry in your hand ... In short, there is undoubtedly a pull toward the mean which keeps all living things within some more or less fixed limitations.

Partner of Nature (1939), page 92. Note that Burbank did not even consider the prospect of creating a new species. His comments are reminiscent of the quaint eight-word poem by Gertrude Stein: "A rose is a rose is a rose." It is useful, before presenting my next skeptic, to place Darwinism in historical perspective. In 1900 Gregor Mendel's work was rediscovered and with it a great impetus was given to Darwinism.With the recognition of Mendel's factors, which we now know as genes, variation among the individuals of a species was no longer a mystery. A major exponent of the new science was William Bateson, now regarded as the founder of modern genetics (he coined the term himself). His enthusiasm for Mendelism was such that he named his newborn son Gregory in 1904. However, that enthusiasm faded toward the end of his life, as Gregory would recount to Arthur Koestler in 1970. By 1924, [William] Bateson had come to realize, and told his son in confidence, "that it was a mistake to have committed his life to Mendelism, that this was a blind alley which would not throw any light on the differentiation of species, nor on evolution in general." *The Case of the Midwife Toad* (1971), page 121. I feel that this is one of the most significant comments in all ofthe evolutionary literature, and it is one with which I totally agree. It is a testimony to the greatness of Bateson that he had the insight to recognize and the courage to admit that failure. Mendelism is, of course, the genetics associated with sexual reproduction, and here we have Burbank and Bateson independently challenging the capacity of that process to result in significant evolutionary change. Note Bateson's use of the expression *blind alley*. Thus, when asked the question -- Can sexual forms evolve? -- one is compelled, on the basis of an overwhelming body of negative evidence, coupled with virtually no positive evidence, to answer -- No, they cannot evolve. This leads to other questions. Is there a kind of reproduction other than the familiar sexual or Mendelian variety and could this alternative mode be an effective evolutionary device? As will become apparent, the answer to these two questions is yes.

III. It is not the genes but the chromosomes that do the evolving

We have long been seeking a different kind of evolutionary process and have now found one; namely, the change within the pattern of the chromosomes. ... The neo-Darwinian theory of the geneticists is no longer tenable. -- Richard B. Goldschmidt

III-1. Chromosome structure and evolution

One of the first to recognize the evolutionary significance of chromosome structure was the geneticist Richard B. Goldschmidt. In 1940, two years before Huxley's *Evolution: The Modern Synthesis*, Goldschmidt published *The Material Basis of Evolution*, based on the Silliman lectures he had delivered at Yale University. It is difficult to imagine two books more dissimilar while dealing with the same subject. Goldschmidt's book is divided into two sections, the first dealing with what he called microevolution, the second with macroevolution. His first section ends with this statementso reminiscent of Bateson: Subspecies are actually, therefore, neither incipient species nor models for the origin of species. They are more or less diversified blind alleys within the species. The decisive step in evolution, the first step toward macroevolution, the step from one species to another, requires another evolutionary method than the sheer accumulation of micromutations. Note Goldschmidt's use of the term *blind alley*, a characterization offered independently by both Huxley and Bateson. Twelve years later, Alexander Petrunkevitch endorsed Goldschmidt'sview on speciation and again employed the term *blind alley*: Without prejudice toward the studies on such animals as *Drosophila*, I believe that Goldschmidt is right when he considers microevolution to be a "blind alley". All morphological evidence is in favor of the assumption that macroevolutionary changes in the Diptera were completed in the comparatively distant past. "Macroevolution and the fossil record of Arachnida" (1952) The "other method" to which Goldschmidt refers is the reordering of existing genetic information within the structure of the chromosome. Alterations in genic expression resulting from such rearrangements are called position effects. In his words at the end of the section on macroevolution: The fact remains that an unbiased analysis of a huge body of pertinent facts shows that macroevolution is linked to chromosomal repatterning and that the latter is a method of producing new organic reaction systems, a method which overcomes the great difficulties which the actual facts raise for the neo-Darwinian conception as applied to macroevolution. *The Material Basis of Evolution* (1940) There are several kinds of chromosome rearrangements. Two chromosomes can fuse together to form one or a chromosome can dissociate to form two. Two breaks can occur along a chromosome with the broken fragment undergoing a 180-degree rotation before reattaching. There are two types of such inversions depending upon where in the chromosome they occur. Each chromosome has somewhere along its length a place where the spindle fibers attach during mitosis and meiosis. This structure, called the centromere, contains DNA and, like the chromosome is also self-replicating. If the centromere is within the inverted segment itis called a pericentric inversion. If the inversion does not include the centromere it is termed a paracentric inversion. Another type of restructuring is reciprocal translocation in which two different chromosomes exchange parts. Other types of changes include duplications and deficiencies. Alterations can also occur in the number and position of nucleolar organizers as well as changes in the chromosome ends or telomeres. Before proceeding I will briefly discuss the irreversibility of evolution as it relates to chromosome structure.

III-2. Why is evolution irreversible?

The curve of evolution demonstrates that it is the result of aseries of irreversible historical phenomena. -- Pierre Grassé. *If we look closely at this truly historical character of evolutionand the uniqueness of its individual stages, irreversibility appears simply as a "self-evident" truth.* -- Otto Schindewolf.

Once more we witness identical conclusions, this time by Grassé, a Frenchman and Schindewolf, a German, with neither referring to the other. No mammal has ever evolved into a reptile, no reptile into an amphibian and no amphibian has ever evolved into a fish. There is not a single documented example of a reversible evolutionary event of any significant magnitude. Why? Point mutations (base pair substitutions) of individual genes are reversible and that alone indicates that such changes do not playa significant role in evolution. By way of contrast, consider an inversion. If such a change should occur, the probability of it being reversed is virtually zero since the chromosome would have to break in exactly the same two places in order for it to return to its original configuration. A similar argument applies to the improbable reversibility of chromosome fusion, dissociation or reciprocal translocation. Furthermore these structural changes are all-or-none events which have no intermediate states and cannot possibly be regarded as gradual. Accordingly, one might anticipate that these effects might be quite dramatic although unpredictable. Incidentally, this perspective also offers an explanation for the absence of transitional forms in the fossil record.

III-3. The first meiotic division

The ideal situation might be for an organism to simultaneously reproduce its own genotype and produce trial balloons as well. It is with this potentiality that a major significance of diploidy becomes apparent. When a haploid creature undergoes a heritable change it has lost its original genetic identity. That is not the case for a diploid organism. To understand this important distinction it is only necessary to realize that there are three self-replicating elements involved. The first of these are the chromosomes, the second are the centromeres and the third are the centrioles, the structures at the ends of the spindles on which the chromosomes move. In mitosis the centromeres and the chromosomes replicate in synchrony so that the daughter chromosomes pass to opposite poles of the mitotic spindle.

The result is that the two daughter cells receive identical sets of genes, becoming thereby clones of the original cell. In the first meiotic division the centromeres do not duplicate when the chromosomes do with the result that the two sister (identical) chromosomes (dyads) *must remain together* during the first meiotic division.This feature lies at the heart of the semi-meiotic hypothesis.

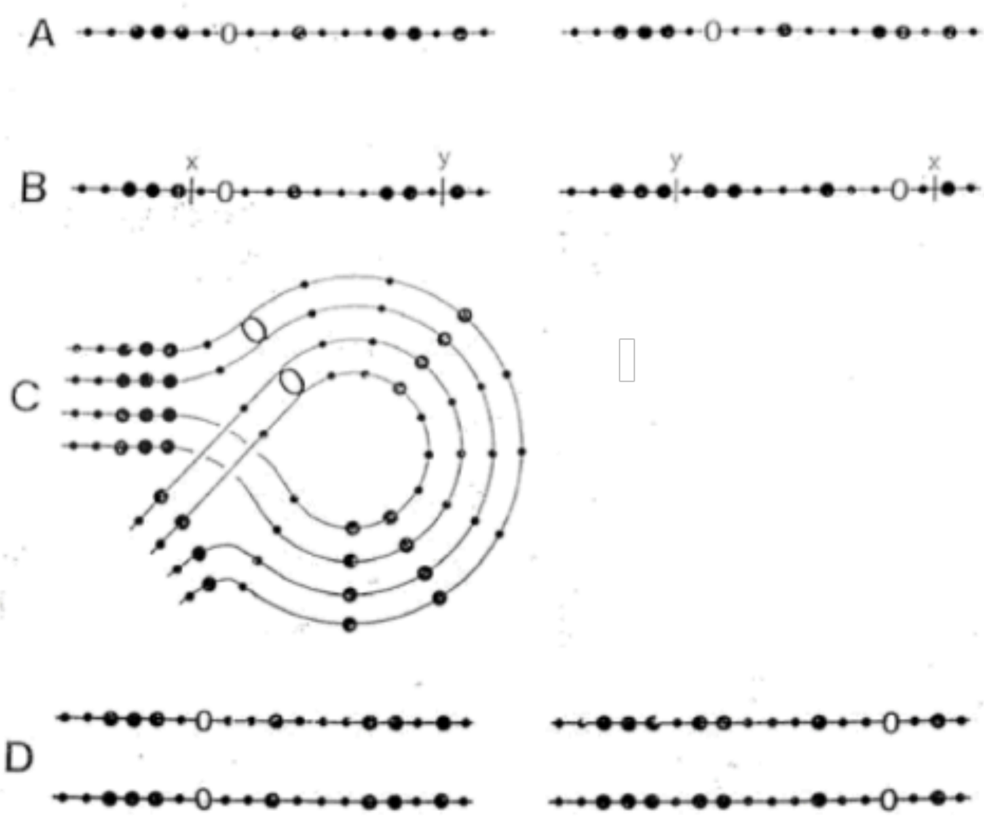

Figure 1. A diagram to illustrate the instantaneous formation of a new chromosome pair following the occurrence of a single pericentric inversion. O represents the centromere .A. The original chromosome pair. B. The inversion heterozygote. C. The tetrad configuration prior to the first meiotic division.D. The products of the first meiotic division following the duplication of the centromeres. From Davison (1984).

Consider an oocyte about to undergo meiosis. Assume further that this oocyte has one chromosome which has undergone an inversion. When the tetrad is formed at synapsis **(Figure 1)** it will consistof two daughter chromosomes (sister strands or dyads) of originalstructure and two daughter chromosomes each containing the inversion. In the first meiotic division one pair of sister strands is discarded into the first polar body leaving the other pair in the egg. If the inverted pair is discarded, the oocyte retains the original genome.

If the normal pair is discarded the oocyte has *instantly* acquired a new karyotype in homozygous form and, following the duplication of the centromere (which results in the separation of the chromosomes) an evolutionary potential as a new kind of diploid organism. All genetic (evolutionary) changes originate in individual cells, in individual chromosomes, in a particular organism. The evolutionary significance of the individual will become apparent in a later section. If the inversion in the above example occurred in a cell destined to become part of the female reproductive lineage, then at the termination of the first meiotic division, one half of the products of that lineage will be like the original and one half will be a potentially new kind of organism with a new paired (homozygous) chromosomal genotype (karyotype) produced in a single cytogenetical step. In this system the only requirement is for one or more oogoniato be heterozygous. Such an evolving series would be expected to produce a number of discrete products determined by the number of chromosome rearrangements involved in the series. I do not suggest that all new chromosome homozygotes would be new species. In fact we know that is not necessarily so. Nevertheless, this perspective is worthy of further attention.

III-4. Position effects and primate evolution

In Goldschmidt's day the internal structure of chromosomes was not well known and was limited in large extent to the giant salivary chromosomes of the fruit fly *Drosophila*. New staining techniques allow a much more detailed analysis of chromosome structure in many life forms. Of special interest are the chromosomes of the order Primates to which we belong. We are fortunate in having three close relatives with which comparisons can be made: the chimpanzee, the gorilla and the orangutan. The higher primates are also interesting because they are among the most recent evolutionary products and accordingly their karyotypes are likely to have retained their original configurations.

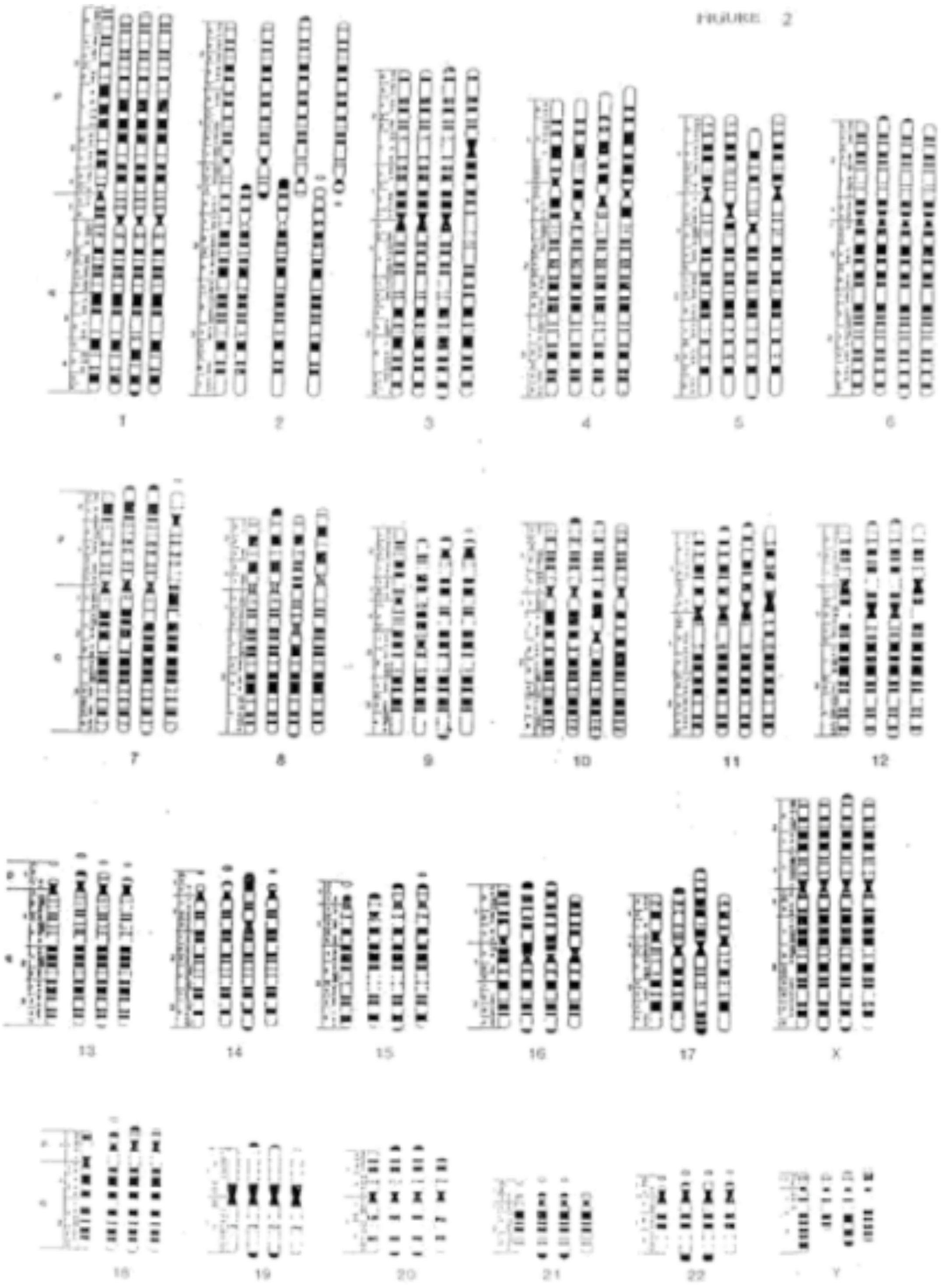

Figure 2. Schematic representation of late-prophase chromosomes (1000-

band stage) of man, chimpanzee, gorilla and orangutan, arranged from left to right, respectively, to better visualize homology between the chromosomes of the great apes and the human complement. From Yunis and Prakash (1982).

In 1982 Yunis and Prakash published a paper entitled "The Origin of Man: A Chromosomal Pictorial Legacy", in which the karyotypes of man, chimpanzee, gorilla and orangutan are compared **(Figure 2)**. The karyotypes are remarkably similar providing convincing evidence that we are all four related. The narrowed region of each chromosome marks the position of the centromere, the structure to which the spindle fibers attach during mitosis and meiosis. The differences that can be recognized are largely structural rearrangements.

For example the three apes have 48 chromosomes while we have 46. This has apparently resulted from the fusion of two of the ape chromosomes to form a single human chromosome (chromosome 2). Some of the differences consist of paracentric and pericentric inversions of homologous chromosome segments as well as variations in heterochromatin. As examples, chromosomes 4, 5, 9, and 12 of man and chimpanzee each differ by a pericentric inversion. Certain chromosomes exhibit reciprocal translocations. Other differences include alterations in chromosome ends or telomeres as well as variations in the position of nucleolar organizers (Yunis, J.J. &Prakash, O. 1982). The original paper should be consulted for the details.

The important point is that the differences which are evident are precisely of the sort that Goldschmidt described: namely, the restructuring of existing genetic information. Under close examination of the karyotypes, the X chromosomes reveal very few differences. This is exactly what one might expect if the four species were linked gynogenetically. By way of contrast, the male-determining (Y) chromosomes lack, both quantitatively and qualitatively, the semblance one would expect had the four genera evolved through sexual reproduction.

Also there are very small differences in both DNA and protein composition between ourselves and our living relatives (Andrews 1987), further supporting the view that conventional (point) mutations maybe of little or no significance in the evolutionary process.

IV. Sexual reproduction limits evolutionary change

All great truths begin as blasphemies. -- George Bernard Shaw

IV-1. The independent origins of sexual reproduction

In the Darwinian or sexual model, one might anticipate some universal sex-determining mechanism operating throughout evolutionary history. If, as I believe, the role of sexual reproduction is to limit evolution, one would anticipate a wide variety of sex-determining devices evolving independently. Such is the actual case. I found that the idea of an independent sexual evolution had already been expressed. The Russian cytologist N.N. Vorontsov was one of the first to call attention to the independent evolution of sex determination. Just as the transition from isogamy to anisogamy and to oogamy took place independently of each other in the various phyla of plants so the formation of mechanisms of the cytogenetical sex determination with differentiated heterochromosomes follows the same pattern in various kingdoms and phyla and results in an independent occurrence of the XX-XY system in *Melandrium* as well as in many Insects and Mammals, whereas the ZW-ZZ system evolved independently in Trichoptera, Lepidoptera, Serpentes and Aves. Against the background of these facts it is unclear whether the male species of different groups are homologous to each other or not; they appear to be nonhomologous. "The evolution of the sex chromosomes" (1973), page 646 Notice the last sentence in which Vorontsov indicated that males seem to be nonhomologous, a conclusion that would, by definition, demand that they were independently produced and accordingly could not be involved in a macroevolutionary continuum.

In addition to the devices mentioned by Vorontsov, other mechanisms have also independently evolved. In the social insects the female is diploid, the male haploid, a situation also found in rotifers. In addition to these chromosomal mechanisms, the temperature during sensitive developmental stages can serve to determine the sex as in some turtles and crocodilians. Sex reversal occurs in certain animals. Young oysters are male and transform into females when they grow larger (protandry). This literature has been reviewedby Bull (1983). Not only are the cytological mechanisms of sex determination often nonhomologous but the expression of the sexual phenotype may also be nonhomologous. For example, both *Drosophila* and all mammals have a heteromorphic (different form) XY male - XX female system. However, sexual differentiation is mediated at the local cellular level in *Drosophila* but by means of hormones in all mammals. It is obvious that the two systems are in no sense related, but must have evolved independently.

This is hardly the situation one would expect if sexual reproduction were a requirement for evolutionary change. I think the most reasonable explanation for this great diversity is that the evolutionary steps involved in macroevolution were made prior to the differentiation of obligatory sexual devices and, accordingly, must have been gynogenetic (presexual) in nature, involving only the first meiotic division. Viewed in this way the evolution of exclusively sexual means of reproduction became the self-limiting step in the evolutionary process. I regard this conclusion as inescapable as I am unable to provide an alternative interpretation to these undisputed facts.

IV-2. The importance of nonhomology

Treasure your exceptions. -- William Bateson. *Irrationally held truths may be more harmful than reasoned errors*. -- T.H. Huxley. Homologous structures have a common origin. The same can be said for homologous mechanisms. Any rational evolutionary hypothesis must recognize, and incorporate into its fabric, nonhomology when that becomes evident. Another example of nonhomology that correlates favorably with the various sex-determining devices is the origin of the definitive germ cells in contemporary vertebrates.

One of the hitherto most baffling features of vertebrate ontogenyis offered by the origin of those cells (oogonia and spermatogonia) destined to become the eggs and sperm. Again it is useful to place evolutionary theory in historical perspective. August Weismann (1891) is well known for having predicted meiosis and for his interesting aphorisms such as: "The protozoa are immortal"and "From eagle eggs come eagles". Each of these statements implies reproductive continuity which is, of course, required for any theory of evolution.

However, Weismann extended his hypothesis further with his notion of the *continuity of the germ plasm*. According to this concept there has been an unbroken chain of reproductive cells which through modification have produced the many life forms that have existed, a chain that exists to the present day. Evolution does not demand a continuous cell lineage but only *reproductive continuity* from one generation to the next. The actual facts are as follows. In birds the cells destined to become the germ cells first appear in the extra-embryonic endoderm (germinal crescent) anterior to the head of the developing embryo. Incidentally, this region has no homologue in the hatched bird as the extra-embryonic endoderm is, by definition, resorbed as nutrient for the developing chick. From there the presumptive germ cells enter the circulatory system and, after a period of time in the bloodstream, penetrate the walls of the venous circulation and invade the gonad where they differentiate into the definitive gametes. In mammals the presumptive germ cells first appear in the endoderm of the allantois, a structure destined to become the urinary bladder of the adult. From here they migrate in amoeboid fashion anteriorly and laterally to reach the gonad where they complete their differentiation. Thus, there is no way that the reproductive cells of mammals can be homologized with those of birds as they originate from opposite ends of the embryonic axis and reach the gonads by completely different means.

Similarly, the eggs and sperm of the Anura (frogs and toads) arise in an entirely different way than do those of the Urodela (salamanders and newts). Staining methods reveal that in frogs, the cells destined to become the germ cells result from the presence of preformed granules near the vegetal pole of the unfertilized egg, a region destined to become part of the endoderm. From there they move first dorsally and then laterally to enter the embryonic gonads which are mesodermal structures. In salamanders the presumptive germ cells first appear in the mesoderm as a result of the inductive action ofthe underlying endoderm on the lateral plate mesoderm. From there they migrate medially to invade the embryonic gonads. Thus the germ cells of the Anura and the Urodela do not even arise from the same germ layer! In short, there is not a scintilla of evidence to support the notion of germ cell continuity. The details of these differences have been discussed elsewhere (Davison 1984). Also, the vertebrate gonad is a sterile organ unable to produce germ cells from its own epithelium (Nieuwkoop and Sutasurya 1979). Instead, the test is orovary receives its complement of eggs or sperm by a process of invasion from extragonadal sources early in development. Since the sources and modes of invasion are not homologous from group to group, the continuity of the germ plasm is a myth. As someone so aptly put it: "Hypotheses have to be reasonable -- facts don't. "Note that these nonhomologies correlate favorably with the nonhomologous devices that now serve to determine the sex differences. In order to deal with all this, it is necessary to postulate that contemporary reproductive cell lineages cannot be ancestral but have independently replaced the original (semi-meiotic) lineage and that the latter is no longer extant. We may never know the source of the original cell lineage but a very reasonable guess might be the gonadalepithelium, a tissue that has since become sterile. I can conceive of no other way to cope with these realities.

IV-3. Semi-meiosis and the origin of diploidy

One of the most significant events in evolutionary history was the transformation from haploidy to diploidy since, as I have indicated, diploidy allows the retention of the original genome at the same time that it permits new configurations to be produced as a result of the first meiotic division. The transformation from haploidy to diploidyhas probably occurred many times. One such transformation bears directly on the significance of the first meiotic division as an evolutionary device. In 1947, L.R. Cleveland published a short but highly significant paper dealing with the origin and evolution of meiosis. Oddly enough, this paper has gone virtually unnoticed. His material was the various flagellate protozoa that live as commensals in the guts of wood-eating insects. Of particular significance here are his observations on the flagellate genus *Spirotrichosoma* which is found in three species of *Stolotermes*, a primitive termite genus with species in Australia, New Zealand and South Africa. The haploid number is 12 in *Spirotrichosoma* and haploids are found in all three locales. However, in addition, polyploids with 24, 48 and 60 chromosomes are found only in the New Zealand populations. Clearly, we are observing the evolution from haploidy to diploidy and polyploidy in the New Zealand material. I quote Cleveland: Nuclear division of these polyploids can be seen very plainly, especially those with 4 rod-shaped chromosomes. Every division is exactly alike: synapsis in the prophase, followed by formation of tetrads, and movement of the chromosomes to the poles as dyads, *i.e.* every division is exactly like the first division in meiosis. "The origin and evolution of meiosis" (1947). Following this single nuclear division the centromeres duplicate allowing the sister chromosomes (dyads) to separate. The cycle then repeats. Note that these animals have no sexual phase since the second division never takes place. Accordingly, they present a living example of the semi-meiotic mechanism. These observations also suggest that the first meiotic division may be a more primitive form of reproduction than diploid mitosis (Davison 1984 1993).

IV-4. Semi-meiosis in birds

Another example of semi-meiosis is offered by the Beltsville strain of small white turkey which produces a low but significant percentage of its offspring parthenogenetically (Olsen 1965). The proof that the mechanism is semi-meiotic is that all of these offspring are males. In birds, it is the female that is heterogametic (ZW) while the male is homogametic (ZZ). The Z chromosome is larger than the W chromosome, just as the X chromosome is larger than the Y chromosome in mammals. Prior to the first meiotic division the synaptic tetrad consists of ZZ and WW dyads (sister strands). If, during the first meiotic division, the ZZ dyad enters the polar body leaving the WW dyad in the egg, the embryo fails to complete development. (WW is apparently lethal in birds.) If the WW dyad passes into the polar body and the ZZ dyad remains in the egg, it must develop as a male which is the actual case. This example also serves to demonstrate the instantaneous production of a chromosome homozygote from a single heterozygous source. If birds, like mammals, had homogametic females, the parthenogenetic turkey, in theory at least, would be capable of progressive evolution at the same time that it could retain its original genetic (species) constitution! There is another curious fact that lends credence to the semi-meiotic hypothesis. Since spermatozoa are universally haploid in their functional state, one might anticipate that the same would be true for the mature ovum. Such is not the case. The vast majority of animal eggs are unreduced at the time the sperm enters. The egg at this time has often produced the first polar body and is arrested in metaphase of the second meiotic division and so is still diploid as it has completed only the first meiotic division. This is the case for most, if not all, vertebrates including *Homo sapiens*. I have suggested that this might represent an evolutionary relic from a time when the sperm either was not necessary for activation or served only as an activator without contributing genetic information (Davison 1984). Such a reproductive mode would be, by definition, semi-meiotic. In any event, some agency other than the sperm serves to activate the egg of the parthenogenetic turkey.

IV-5. Sex reversal in birds and amphibians

It is obvious for cytogenetic reasons why only male turkeys can be produced by means of the first meiotic division. Birds demonstrate another important feature of sex differentiation. It has been known since antiquity that hen chickens occasionally transform into crowing roosters. In birds, while both testes are present in the male, females have only a single ovary, the left one. If the ovary is destroyed by disease or is surgically removed, the other potential gonad is relieved of inhibition (derepressed) and can then develop into a testis. This is possible because of the bipotential nature of the vertebrate gonad. Like the kidney and adrenal gland with which it is developmentally associated, the embryonic gonad consists of an outer cortex and an inner medulla. Normally, the genotype determines which of these will develop. The cortex becomes the ovary and the medulla the testis. Each functional gonad serves to inhibit the development of the other (Witschi 1956). The bipotential nature of the vertebrate gonad is also demonstrated by observations on the development of frogs. Frogs (*Rana* species), while they lack heteromorphic (visibly different) sex chromosomes, can be shown to have heterogametic (XY) males like humans by rearing the tadpoles in the presence of small amounts of male hormone (methyltestosterone). The male hormone overrides the genetic constitution so that all of the animals, both XY and XX, develop into fertile males. When the XX males are crossed with XX (normal) females they produce mostly, but not exclusively daughters, demonstrating that even in sexual reproduction the female genome is capable of producing both sexes. Similarly, genetic males may be transformed into females by rearing the larvae in the presence of female (estradiol) hormone (Witschi 1956). Normally, the sex of frogs is determined at the moment the sperm enters the egg which, in nature, is instantly as the eggs are extruded into the pond water which is already charged with sperm released by the male partner. Early in this century Richard Hertwig discovered that, if fertilization is delayed, an excessive number of males are produced, again demonstrating the bipotentiality of the gonad (Wilson 1925). In 1916, Jacques Loeb induced several thousand frog eggs to divide by pricking them with a fine needle. The vast majority of the embryos proved to be haploid and never completed larval development, but twenty were successfully raised to maturity and were shown to be diploid, undoubtedly due either to the occasional failure of the second meiotic division to take place or to the reentry into the egg of the second polar body nucleus (Wilson 1925). Thus these frogs were produced semi-meiotically. Of the 20 frogs, 15 were males, 3 were females and 2 were of uncertain sex. The preponderance of males is to be expected in light of Hertwig's observations on delayed activation. More recently, large numbers of gynogenetic frogs have been produced by utilizing sperm irradiated with ultraviolet light. These sperm serve to activate the egg to complete meiosis and proceed with development but the sperm contribute no genetic information. Following activation the eggs are heated briefly which serves to suppress the second meiotic division. This procedure produces large numbers of gynogenetic normal diploid frogs. Thus these animals are examples of experimentally induced semi-meiosis. As with Loeb's experiments these are not all female with about 3.5 females to each male. These males remain, of course, genetically female (XX) and, when crossed with normal (XX) females, produce primarily but not exclusively daughters. As with hormonally sex-reversed (XX) males, approximately one in twenty of their progeny is a male (Nace and Richards 1969). These findings are significant because they demonstrate convincingly that all of the necessary genetic information for both sexes is contained in the female genome. It is significant that transformed (XX) male frogs are fertile, and the fertility is independent of the means by which they were produced, whether by hormonal transformation, experimental gynogenesis or delayed fertilization. The last two means probably have the same temporal basis involving delayed activation. The capacity of the female genome to produce both sexes is not limited to the vertebrates since it is also demonstrable in the social insects, water fleas (Cladocera) and rotifers just to mentiona few of many invertebrate examples. The same capacity is obvious in all monoecious (hermaphroditic) organisms, examples of which occur throughout both the animal and plant kingdoms.

IV-6. Semi-meiosis and genetic variability

The gynogenetic offspring from a common mother are also interesting from the point of view of semi-meiosis as a device for generating genetic diversity. Frogs, like mammals, have evolved immune systems and will reject a skin transplant from a genetically different donor. Gynogenetically produced siblings reject skin transplants from one another. They also reject skin transplants from their common mother because none of them have all of her genes. In fact they each have exactly one half (qualitatively) of her total genetic constitution, the other half having been eliminated in the first polar body.The mother will, however, accept a skin transplant from any of her gynogenetic progeny because none of them have any genes that are not hers (Nace and Richards 1969).There are two sources of the genetic diversity generated by semi-meiosis. The first is the random segregation of maternal and paternal dyads (sister strands) that has taken place as a result of the first meiotic division. Frogs (*Rana*) have 13 pairs of chromosomes. Accordingly there are 2 raised to the 13th power or 8192 possible combinations. For humans, with 23 pairs of chromosomes, the number of combinations becomes 8,388,608. The second source of variation is due to crossing-over (exchange of chromosome segments between non-sister strands) which has preceded the first meiotic division. Thus the genetic diversity generated during the first meiotic division is, for all practical purposes, limitless. While it is true that semi-meiosis can produce new structural chromosome pairs (homozygotes), it is not true that it necessarily leads to gene homozygosity. In sexual (Mendelian) reproduction, in the absence of selection, heterozygosity can never exceed 50% even if one starts with 100%, as in crossing two heterozygotes, since it is immediately reduced to 50%. This limitation does not apply to the first meiotic division. Through experimental gynogenesis one can detect heterozygosity by employing heterozygous females and then inhibiting the second meiotic division. Lindsley *et al* (1956) found cross-over (heterozygote) frequencies of 0.688, 0.694 and 0.724 for three characters in the axolotl (a urodele amphibian) and Davison (1961) found a frequency of 0.78 for the Burnsi locus in the frog *Rana pipiens*. The only requirement for this result is that the genes be at an appropriate distance from the centromere which apparently is the case for these four genetic loci. Accordingly, for some genes at least, heterozygosity can substantially exceed that possible by means of sexual reproduction. By this I do not mean to imply that heterozygosity necessarily confers some adaptive advantage as I am not at all certain that is the case.

V. The failure of the Darwinian hypothesis

Let us give nature a chance; she knows her business better than we do. – Montaigne *Nothing is more damaging to a new truth than an old error.* -- Goethe

V-1. Darwin's finches Since the Darwinians have chosen to ignore the semi-meiotic hypothesis, I will introduce what I must imagine their objections might be and then comment on the evidence for that perspective. The Darwinian or sexual model has restraints that are necessary for it to succeed. The achievement of both gene and chromosome homozygosity require that the genetic alterations occur in small isolated populations. This is necessary because the probability of two heterozygotes mating would be very small in a large population. Incidentally, the semi-meiotic model has no such restraint. The Darwinians might simply say that the sexual model could also produce chromosome and gene homozygosity through the inbreeding associatedwith small or insular populations. It is precisely here that their hypothesis fails. For example, the biota of the Galapagos Islands closely resembles that of neighboring Ecuador. Darwin's celebrated finches have all been placed in the genus (or subgenus) *Geospiza*. Since they are all extremely similar, it is not surprising to learn that they produce spontaneous fertile and genetically fit hybrids (Grant and Grant 1994). Thus, by a physiological criterion they are one species and, as with dogs and goldfish, no significant evolution has really taken place.

They too reproduce sexually. There is another difficulty with the sexual model when one considers chromosome restructuring. Consider a chromosome pair heterozygous for a paracentric inversion. A single cross-over within the inversion loop will lead to the formation of an acentric and a dicentric chromosome, while the same kind of cross-over occurring in apericentric inversion heterozygote leads to two monocentricchromosomes each carrying a deficiency and a duplication. All such gametes can be expected to result in a lethal zygote (White 1973). In short, chromosome restructuring is simply not compatible with sexual reproduction. In fact, sexual reproduction tends to prevent rather than promote chromosome restructuring as chromosomere structuring leads to a lower reproductive efficiency due to the deleterious effects of crossing-over prior to the first meiotic division. Note that in the semi-meiotic model the new chromosomehomozygote need only be produced once since the capacity to gynogenetically generate both sexes has been clearly demonstrated in the material already described and may have been a common feature of macroevolution in the past. Once the new chromosome homozygote has been produced the deleterious effects of crossing-over immediately disappear and only re-manifest when one member of the new chromosome pair undergoes a further structural change.

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V-2. The evidence from cytogenetics

The great tragedy of Science -- the slaying of a beautiful hypothesis by an ugly fact. -- T.H. Huxley. I fail to understand why Huxley would have considered such a revelation as tragic. Facts and facts alone remain the basis for all true progress and accordingly they can only be beautiful-- never ugly! Stated another way -- How can a hypothesis be regarded as beautiful when it does not conform with the facts? Any hypothesis of organic evolution must stand in accord with the realities of cytogenetics. What is critically relevant to the argument presented here is a simple question: Were chromosome restructurings effected sexually, as the Darwinian view demands, or were they produced by some other means? The Australian cytologist Michael J.D. White had a number of very pertinent remarks to make on this issue. Here are several which go directly to the very heart of the matter: The conclusion we must draw from these facts (and a great many more instances of the same kind in beetles, mammals and in fact *in almost every group of animals whose chromosomes have been studied*) is that, in certain groups at any rate, fusions and dissociations which exist as cytotaxonomic differences between species *have not been preceded* by a condition of balanced polymorphism in an ancestral population. (my emphasis) *Animal Cytology and Evolution* (1973), page 765. It seems safe to predict that any discussion of the broad mechanisms of evolution in, say, twenty-five years' time, will have to take far more account of the chromosomes themselves as bodies composed of nucleic acid and proteins, and their relations to the rest of the cell at various stages of mitosis and meiosis. And, as indicated earlier, it will almost certainly lay more stress on the role of chromosomal rearrangements in *initiating and promoting speciation*. (my emphasis) Ibid., page 783. Referring to the many chromosomal rearrangements that have occurred in the evolution of the species in the genus *Drosophila*, White offered the following comment. The evidence in favor of the view that many cytotaxonomic differences have arisen without passing through an adaptive polymorphism stage has been growing steadily. Even in *Drosophila* the fifty-eight fusions have most likely established themselves *without benefit of heterosis*. (my emphasis) Ibid., page 768. White's language is unmistakable. He has surmised that the chromosome restructurings were, in all likelihood, not produced sexually. Once again we witness the complete failure of the Darwinian model. I submit that if they were not produced sexually, there remains only one other conceivable way they could have been produced and that is semi-meiotically as I have indicated. If there is another way, I can only hope that someone will enlighten me! I realize that the vast cytogenetic literature is beyond the scope of this essay. Accordingly, in light of the above, I place the burden of proof on the Darwinians by challenging them to present karyotypic, genetic, taxonomic, fossil, or any other kind of evidence indicatingthat true species, genera, families, or any of the higher taxonomic categories *have ever been produced or can now be produced through the agency of sexual reproduction*. I, in general agreement with White, can find nothing in support of that proposition.

V-3. A hypothetical reconstruction of evolutionary history

The following is an attempt to explain the course of evolution while incorporating *all of the preceding verified facts*. Any hypothesis that fails to account for all of the facts is fundamentally flawed and must be considered invalid. It is only necessary to accept the reality that contemporary germ cells cannot be ancestral but must be secondary in origin. It follows that there must have been times when organisms possessed two sources for reproduction, the semi-meiotic lineage which I have described and the sexual lineage which now largely prevails. It is reasonable under those conditions that both modes of reproduction could occur simultaneously. Why then has the original or semi-meiotic lineage largely disappeared? First, while the semi-meiotic mode is ideal for the production of new trial balloons, that could become a disadvantage once a new and successful creature has been produced. Second, sexual reproduction has a potential advantage in its capacity to produce limited variation within a narrow range. The sexual mode could thus be useful in adapting the organism to minor environmental changes. Thus, the sexual lineage might be expected to replace the semi-meiotic lineage in a changing environment. However, severe changes might be beyond the capacity of the sexual mode, leading to extinction. This would seem to be the situation at present when so many species are disappearing. The vast majority of all organisms that have evolved have become extinct. Why? I answer that it may be due, at least in part, to the fact that sexual reproduction is not well suited to the elimination of genetic defects. Nearly all point mutations are deleterious if not lethal; in the sexual mode, they tend to accumulate, leading ultimately to the extinction of the forms in question. Particularly vulnerable are animals that reproduce infrequently, thereby presenting few opportunities for natural selection to cull the genetic defectives. Giant animals, which typically leave few offspring, have been especially prone to extinction, while their smaller and more prolific cousins have survived. In further support of this view, many "living fossils" -- primitive-looking creatures with extraordinary evolutionary longevity -- produce enormous numbers of progeny, ensuring that some will be genetically fit; they also tend to live in the oceans, which are more stable than either the freshwater or terrestrial environments. The bivalve *Ostrea* serves as an example of both strategies, the coelacanth an example of the latter. Obversely, semi-meiosis is admirably suited to the elimination of deleterious genes and gene arrangements since these tend to be exposed as homozygotes. Accordingly, the semi-meiotic lineage could theoretically continue to purge itself of defective genes and gene arrangements as long as it remained in operation (Davison 1993). In support of this interpretation it is interesting to note that newly evolved life forms typically flourish for some time before ultimately declining and becoming extinct (Schindewolf 1993). Life forms that were produced semi-meiotically would, at their inception, be expected to be relatively free of defective genes and gene arrangements since these would have been eliminated as soon as they were expressed and thereby exposed in homozygous form.

VI. Gradualism versus saltationism

Species and the higher categories originate in single macroevolutionary steps as completely new genetic systems. -- Richard B. Goldschmidt. *As mutation always involves leaps or interruptions, we can understand why species, in our sense of the word, should be sharply distinguished one from another*. -- Leo S. Berg

VI-1. The fossil record

Once again we observe virtually identical conclusions drawn, as far as I can determine, independently, this time by Richard Goldschmidt and Leo Berg. Darwinism rests firmly on gradualism and therein resides another of its failures. The fossil record simply fails to support this notion. The semi-meiotic hypothesis, depending as it does on chromosome restructuring, represents the antithesis of gradualism and finds much in the fossil record in accord with its implications. The record often discloses the sudden appearance of *new kinds of living things*. For that reason I think it is more meaningful to emphasize the sudden appearance of a new kind (Genus or higher category) of organism than it is to engage in endless speculation about what constitutes a species. Virtually all the evidence supports Goldschmidt's view that subspecies are "blind alleys" which are in no way involved in the process of macroevolution, a conclusion reached by Burbank, Bateson and Petrunkevitch as well. The four higher primates, man (*Homo*), Chimpanzee (*Pan*), Gorilla (*Gorilla*), and Orangutan (*Pongo*) are all in separate genera. How can they be gradually transformed one into the other when the very differences which they so strikingly exhibit (chromosome reorganizations) by definition have no conceivablygradual or intermediate states? The restructuring of a chromosome, like pregnancy, is an all-or-none event! It is the discrete nature of species that allows an amateur bird-watcher like myself to identify every bird I see with a simple key or even a picture. It is obvious from the absence of intermediate forms that a primary role for natural selection is to prevent variation and accordingly to maintain the *status quo*, a conclusion reached by Punnett long ago as was indicated earlier. On the other hand, the semi-meiotic hypothesis remains in complete accord with evolutionary saltation (from the Latin *saltus*, to leap). Richard Goldschmidt, Leo Berg and Otto Schindewolf all favored saltation as an evolutionary device. This is highly significant because they approached evolution from completely separate directions: genetics, zoogeography and paleontology respectively. Of paramount importance is the agreement that has been reached by Schindewolf and Goldschmidt especially since each drew his conclusions independently. It is dramatically demonstrated in the following excerpt from Schindewolf's *Basic Questions In Paleontology* (German edition 1950, English translation 1993), page 352: Richard Goldschmidt laid out his intellectual edifice in 1940 in an extensive, thoroughly provocative work entitled *The Material Basis Of Evolution*, with which I was not yet familiar when I prepared this manuscript. His earlier communications on this subject have had considerable influence on my thinking or have strengthened it, but in essence, the concepts described here grew out of my own analysis of paleontological material. All the more surprising and pleasing, then, is the broad agreement in our views. "Schindewolf's theory is practically identical with that of Goldschmidt," as D.D. Davis (1949) observed recently based on my 1936 publication. I regard this convergence of views arising from extremely different premises as a welcome sign that we are on the right track. Indeed, Goldschmidt goes further than I and is in a position to support

his phylogenetic conclusions genetically. He holds that microevolution through the accumulation of micromutations is a process that, in adaptation to the environment, leads only to a diversification within the framework of species and does not exceed the boundaries of species. "Subspecies, therefore, are actually neither incipient species nor models for the origin of species. They are more or less diversified blind alleys within the species." According to him, macroevolution would require a different evolutionary mechanism, one that would create the decisive transformational step from species to species, from one higher category into another. It would not take place through a series of atomistic alterations but by way of a far-reaching transformation of intrachromosomal structures. This *repatterning*, or *System mutation*, is attributable to cytologically provable breaks in the chromosomes, which evoke inversions, duplications, and translocations. A single modification of an embryonic character produced in this way would then regulate a whole series of related ontogenetic processes, leading to a completely new developmental type. Accordingly, gross anatomical differences between two taxonomic types would not have to evolve through the simultaneous selection of numerous small mutants as determiners for each individual organ but could arise through a single evolutionary step. This explanatory attempt by Goldschmidt has aroused much opposition among other geneticists. Paleontology has no right to intervene in this dispute. From my personal point of view, I can add only that Goldschmidt's inferences completely meet the challenge that fossil material appears to me to pose, and that he, as a leading geneticist, has presented a complete interpretation that does justice to the tangible, historical phylogenetic data.
Ten years earlier, Goldschmidt had commented on Schindewolf in *The Material Basis of Evolution* (1940), page 395: ... I need only quote Schindewolf (1936), the most progressive investigator known to me, who showed that the material presented by paleontology leads to exactly the same conclusions as derived in my writings, to which he refers. He elaborates the thesis that macroevolution on a higher level takes place in an explosive way within a short geological time, followed by a slower series of orthogenetic perfections, as exemplified in the oft-quoted evolutionary series. He realizes that the conception of preadaptation accounts completely for this type of evolution. He shows by examples from fossil material that the major evolutionary advances must have taken place in single large steps, which affected early embryonic stages with the automatic consequence of

reconstruction of all the later phases of development. He shows that the many missing links in the paleontological record are sought for in vain because they never existed: "The first bird hatched from a reptilian egg." Schindewolf and a few others also realize that the genetical and phenogenetical facts and ideas from which my thesis was derived furnish the basis for an understanding of such a process of evolution. Thus we see that the results of paleontology -- see Schindewolf for references to other authors who have come to similar conclusions -- vindicate the thesis which we developed here. It is gratifying that all the disciplines which furnish material for the understanding of evolution -- taxonomy and morphology, descriptive and experimental embryology, static and dynamic (physiological) genetics, comparative anatomy and paleontology -- supply ample and parallel evidence for a theory of evolution which is more plausible than the neo-Darwinian theory. These excerpts constitute powerful support for saltation as the key macroevolutionary device, and accordingly lend further credenceto the semi-meiotic hypothesis. Leo Berg offered very similar conclusions in a series of 10 comparisons he made between Darwinism and Nomogenesis (evolution according to law) at the very end of his book. Numbers 3, 5, 7and 8 are in complete accord with what has so far been presented here. In each instance the Darwinian view is presented first, followed by Berg's view. 3. Based on chance variations -- based upon laws. 5. By means of slow, scarcely perceptible, continuous variations. -- By leaps, paroxysms, mutations. 7. The struggle for existence and natural selection are progressive agencies. -- The struggle for existence and natural selection are not progressive agencies, but being, on the contrary, conservative, maintain the standard. 8. Species arising through divergence are connected by transitions. -- Species arising through mutations are sharply distinguished one from another. I cannot resist commenting on the quotation that Berg ascribed to T.H. Huxley in the frontispiece to his book: "Science commits suicidewhen she adopts a creed." That has proven to be a remarkably slow form of suicide in the case of Darwinism, which made its debut in 1859 and is still apparently thriving in the twenty-first century!

VI-2. The significance of the individual in macroevolution

The definition of the individual was: a multitude of one million divided by one million. -- Arthur Koestler. *The history of science is science itself; the history of the individual, the individual.* – Goethe. Semi-meiosis, being a gynogenetic process, can have enormous impact as a result of a single occurrence since the unique genome can produce an unlimited number of products including, at least in those forms for which we have good information, members of the opposite sex. The Darwinians place great emphasis on populations as the units of evolution. There is absolutely no rationale for this perspective. As was indicated earlier, all genetic (evolutionary) changes originate in *individual* chromosomes in *individual* germinal cells in *individual* organisms. If a newly evolved creature is able to reproduce itself, it will do so and the numbers of that species will increase. It is as simple as that. Accordingly, population genetics has a questionable place in the evolutionary process. While the Darwinians have emphasized populations, the significance of the individual was certainly obvious to Robert Broom. From his 1933 book, *The Coming of Man* in which he is discussing the origin of the mammals (page 215, my emphasis): A line of small generalized Therocephalians appears to have been successful. They gave rise to a higher group, the Bauriamorphs, and *some member* of this group gave rise to the Ictidosaurians; and from *an Ictidosaurian* arose the first mammal. The little line that ran from the Therocephalians to the first mammals was entirely made up of small animals. Many side branches specialized and became moderately large, but these all soon perished. Only the little generalized types carried on the line, but they always died out as soon as a higher type arose. Probably *only one Bauriamorph* led to the Ictidosaurians, and almost certainly *only one Ictidosaurian* gave birth to the mammalian stem. Apparently in Upper Triassic times *a small Ictidosaurian* -- perhaps as small as a mouse -- developed hair, and about the same time the lower jaw formed a new joint between the dentary and the squamosal bones, and the little bones of the jaw became ear ossicles, and the heart became four chambered. All these changes probably took place nearly simultaneously. We might regard the evolution of one of these characters as a happy accident, but that all should arise about the same time and by accident is incredible. Broom correctly understands that it is the individual which is the unit of evolutionary change.

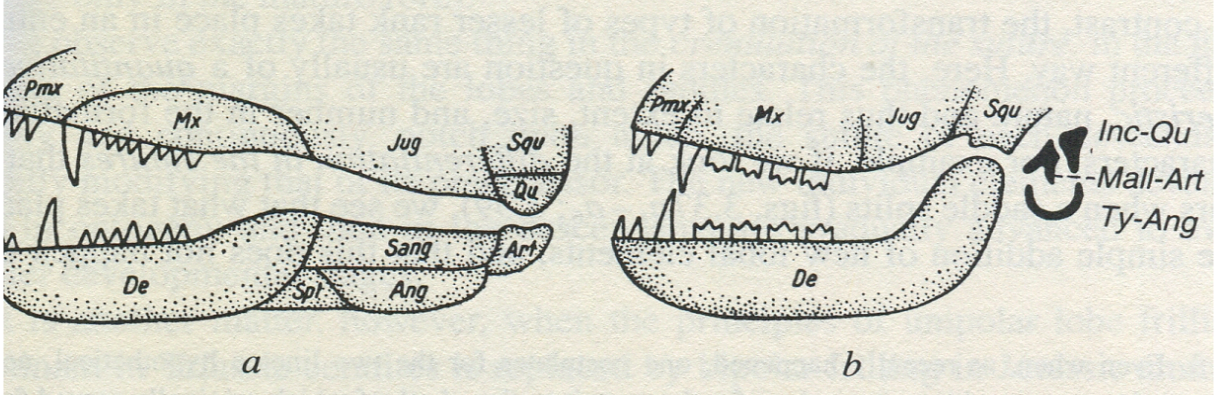

Figure 3. Diagram showing how the reptilian lower jaw **(a)** was refashioned into the mammalian lower jaw **(b)**.*De* = dental; *Spl* = splenial; *Ang* = angular; *Sang* = supraangular; *Art* = articular; *Pmx* = premaxillary; *Mx* = maxillary; *Jug* = jugal;*Squ* = squamosum; *Qu* = quadratum; *Ty* = tympanicum; *Mall* = malleus; *Inc* = incus. From Schindewolf, *Basic Questions in Paleontology* (1993), page 211.

It is revealing to compare Broom's treatment of the origin of the ear ossicles (*malleus* or hammer, *incus* or anvil and *stapes* or stirrup) with the independent and virtually identical conclusions of Schindewolf: *The vertebrate lower jaw*, for example, is composed *either* of several separate parts and joined to the skull by the auricular, as in reptiles **[Figure 3a]**, *or* -- as in mammals -- consists of a single bony element, the dentary, which takes on the function of articulation with the skull **[Figure 3b]**.

Slow, smooth transitions between these *qualitatively* opposing structures taking place during post embryonic developmental stages, when the jaw mechanism must be able to function, are inconceivable. To be sure, we recognize in the reptilian lineages that lead to mammals a gradual, *quantitative* reduction of the articular and of the other individual bones of the lower jaw, paving the way for the transformation and bringing the two types closer together. However, the fundamentally decisive, final step -- the complete disappearance of these bones or their transformation into elements of the auditory area -- must have taken place *discontinuously, suddenly, between one individual and the next, during an embryonic developmental stage*. (Schindewolf's emphasis) *Basic Questions in Paleontology* (1993), pages 211-212This concurrence is extraordinary since neither Schindewolf nor Broom makes any mention of the other which is not surprising considering the language differences. Thus, just as Schindewolf, Berg and Goldschmidthave independently identified saltation as the mechanism for macroevolution, so Schindewolf and Broom have independently, and in my view correctly, identified the individual as the instrumentof evolutionary change. Both of these conclusions are, of course, incompatible with neo-Darwinian theory. It is equally obvious that the individual cannot practice sex, since that act requires two. If not sex, there is left only one conceivable alternative and that is the first meiotic division as I have proposed. Again, the conclusion is inescapable. Since it is the individual that is responsible for evolutionary progress, the rare event can assume enormous significance, a consideration that should be kept in mind when asking the question -- Is evolution finished? Perhaps it is not!

VII. Order versus chaos

Therefore evolution follows a determined direction. -- Leo S. Berg. *The existence of oriented lines is a fact, and not a theoretical view; a line can only be identified and exists solely because it embodies a given trend appearing in individuals which derive from one another and succeed one another in time*. -- Pierre Grassé

VII-1. Are there laws governing evolution?

The above two quotations once again demonstrate the independence with which two eminent scientists, one Russian and one French, and each seemingly oblivious to the views of the other, have reached identical conclusions about the nature of evolutionary sequences. Could this be a simple coincidence and are they both wrong? I do not hesitate to answer no to both questions. I have already mentioned the Law of the Reversion to the Average discussed by Burbank. This would seem to be an anti-evolutionary law since it returns the variants to the original wild type. It is clearly demonstrated by the role natural selection plays when domesticated animals are returned to the wild. The aberrant selected forms rapidly disappear in favor of the more conservative types which come to resemble their more distant ancestors. Leo Berg (1969), as the complete title of his book suggests, believed that all of both ontogeny and phylogeny is determined by law, a conclusion which seems to be shared not only by Pierre Grassé but also by Robert Broom (1933). Since they are all three evolutionary biologists for whom I have enormous respect, far be it from me to challenge their convictions, especially since logic has compelled me (admittedly reluctantly) to that same realization myself. I am simply unable to offer any other interpretation.

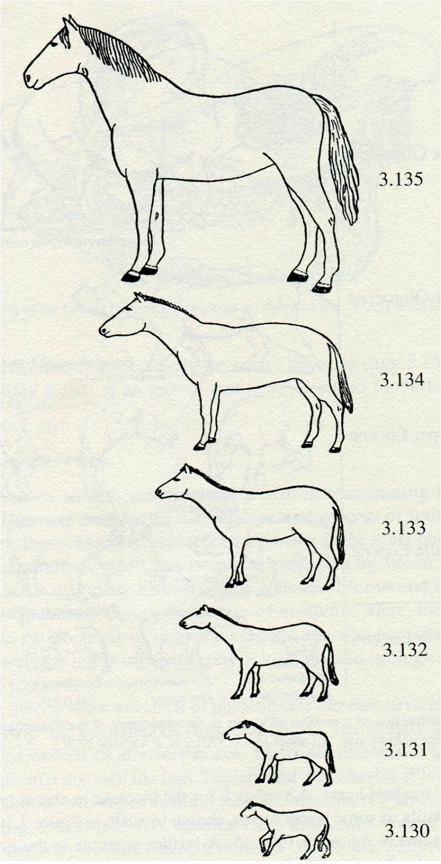

Figure 4. Phyletic size increase in the horse. From bottom to top: *Eohippus*. Lower Eocene. *Orohippus*. Middle Eocene. *Mesohippus*. Oligocene. *Merychippus*. Miocene. *Pliohippus*. Pliocene. *Equus*. Recent.(After R.S. Lull, redrawn.) From Schindewolf, *Basic Questions in Paleontology* (1993), page 292.

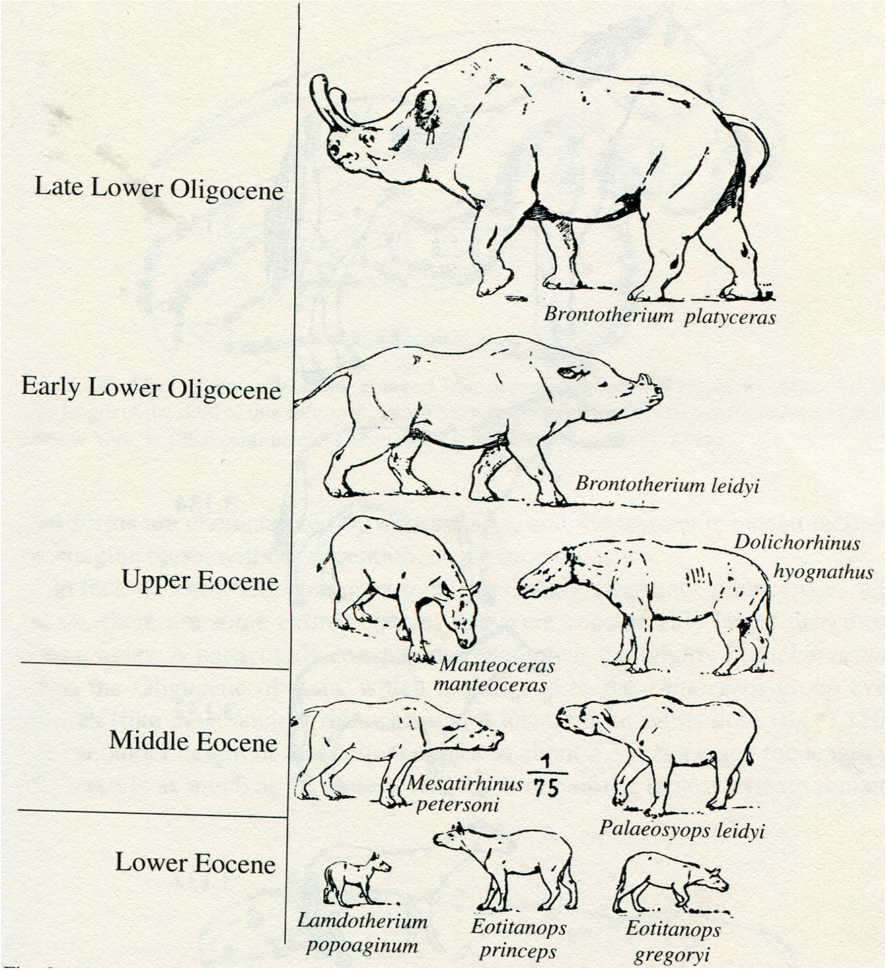

Figure 5. Reconstruction of a number of stages in the phylogeny of the titanotheres showing a progressive increase in body size. (After H.F. Osborn 1929.) From Schindewolf, *Basic Questions in Paleontology* (1993), page 291.

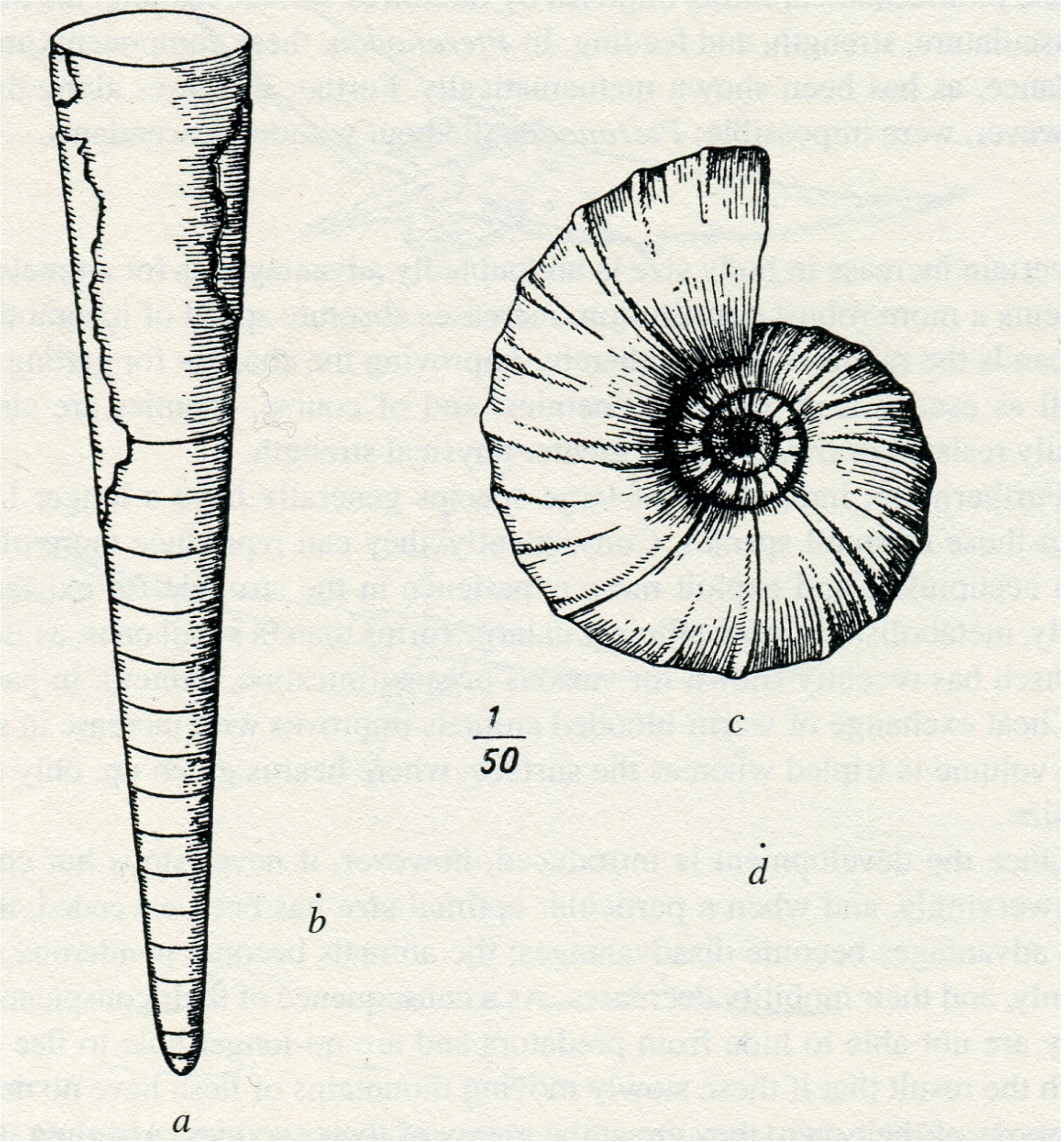

Figure 6. Phyletic size increase in cephalopods. ***a*** shows a very schematic Ordovician *Endoceras*; in contrast, the oldest representative of the Nautiloidea (*Plectronoceras*), shown at the same scale, is represented by the size of the dot above the letter ***b*** and even exaggerated at that. ***c*** gives an idea of the size of the giant ammonite *Pachydiscus*, from the Upper Cretaceous of Westphalia, compared to the average size of the oldest Devonian ammonoids, the dot above ***d***. From Schindewolf, *Basic Questions in Paleontology* (1993), page 298.

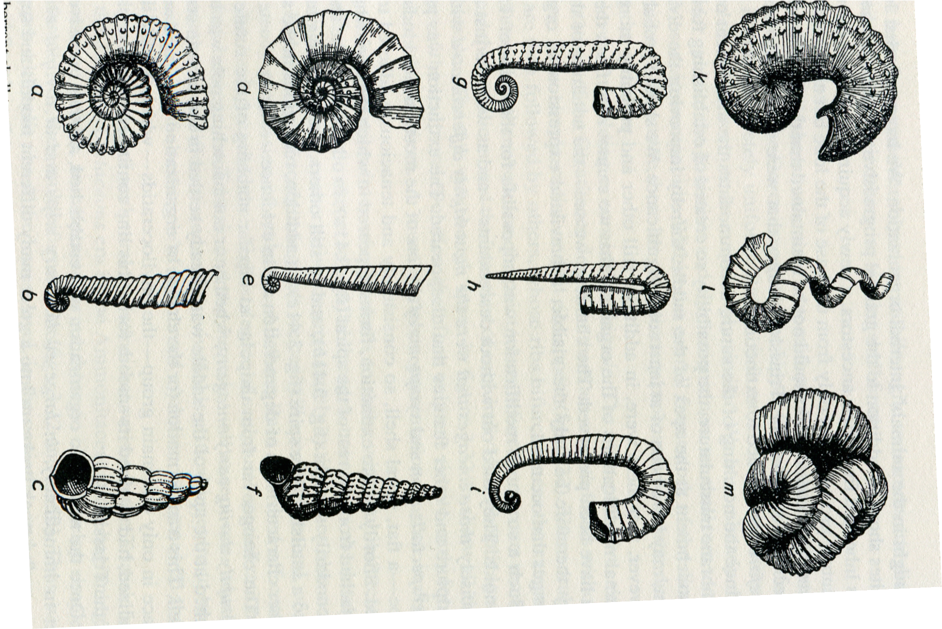

Figure 7. Aberrant shell types of Upper Triassic and Cretaceousammonoids showing the dissolution of form within a stock facing extinction, in some instances with broad similarities of form. *a. Choristoceras. b. Rhabdoceras. c. Cochloceras. d. Ammonitoceras.e. Baculites.f. Turrilites. g. Ancyloceras. h. Hamulina.i. Heteroceras. k. Scaphites. l. Hyphantoceras. m. Nipponites.*(After Janensch, d'Orbigny, Roman, von Zittel, and others.) From Schindewolf, *Basic Questions in Paleontology* (1993), page 142.

There are certain phenomena associated with evolution which, while they might not be described as laws, do characterize much of the fossil record. One of these is orthogenesis or evolution in a definite direction. It is demonstrated with clarity in the evolution of the horse **(Figure 4)** where increase in size and reduction in digits proceed simultaneously.

Another, apparently universal feature of orthogenesis is that new life forms typically appear as small organisms which subsequently become larger and more specialized. This tendency is obvious in dinosaurs, titanotheres **(Figure 5)** and ammonites **(Figure 6)** and has been discussed at length by Schindewolf (1993, page 193). He identified three phases in the evolutionary process which he regarded as having been episodic and cyclic in nature. The first phase which involves the rapid establishment of new forms he termed *typogenesis*. The slower second phase of elaboration and diversification he called *typostasis*.

The third phase, *typolysis*, is characterized by gigantism and overspecialization often coupledwith bizarre morphological developments **(Figure 7)**. This phase ends with extinction. The reality of these phases is well documented but the causes remain obscure. Another common phenomenon is that of convergence. For example, the similarities between the marsupial wolves and bears and their placental counterparts defy any mechanism based upon the accidental production of virtually identical morphologies in unrelated animals. I present an alternative explanation for what has been called convergence in a later section.

VII-2. Epigenesis and preformation

Evolution is in a great measure an unfolding of preexisting rudiments. -- Leo S. Berg *The existence of internal factors affecting evolution has to be accepted by any objective mind.* -- Pierre Grassé

Once again Berg and Grassé independently have concurred on another critical point which cannot be accommodated within the Darwinian hypothesis, since the Darwinians deny the existence of such endogenous factors.

The terms epigenesis and preformation originated from the study of embryonic development. Epigenesis refers to the necessity for embryonic stages to occur in a definite sequence. Thus the formation of the nervous system (neurulation} cannot occur until after the formation of the primitive digestive system (gastrulation). Therefore development is primarily, although not exclusively, epigenetic in nature. These ontogenetic phenomena have interesting counterparts in phylogeny (evolution).

First, with respect to preformation, this concept is clearly favored by what we know about position effects. It is largely the *same genes* which produce a new species when they are rearranged, as is so evident in the primate karyotypes previously discussed. All living things are very similar at the molecular level using virtually identical enzyme systems for the extraction and utilization of energy. The energetic currency (adenosine triphosphate) is universal in both the plant and animal kingdoms as well as in the prokaryotes. At the structural level, the nine plus two arrangement of microtubules is universally the same in all cilia and flagella wherever they are found in the living world. Thus the infinite variety of living creatures can be compared with the variety of combinations that can be obtained from a deck of playing cards in which it is only the arrangement and sequence that are of consequence. The cards (genes) remain the same.

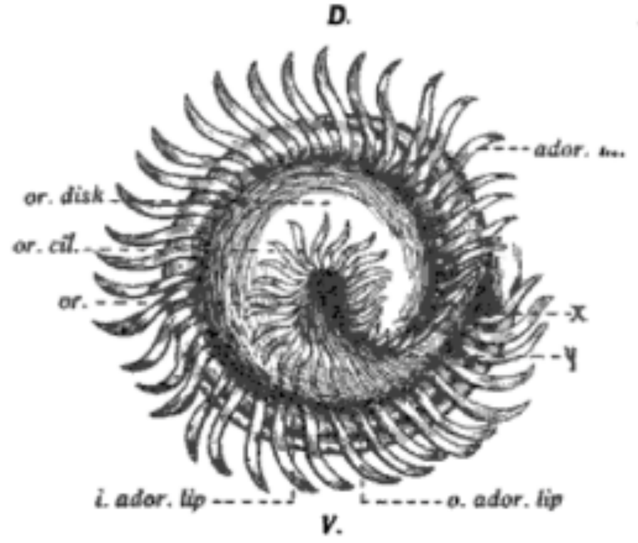

Fig. A. Anterior view of the oral region of *Diplodinium ecaudatum* to show peculiar recurved arrangement of adoral membranelles and oral cilia. × 1150. *ador. m.*, adoral membranelle; *D.*, dorsal side; *i. ador. lip*, inner adoral lip; *o. ador. lip*, outer adoral lip; *or.*, oral opening or cytostome; *or. cil.*, oral cilia; *or. disk*, oral disk; *V.*, ventral side; *X*, beginning of the adoral row of membranelles; *Y*, the point at which the adoral row of membranelles becomes recurved upon itself to form the row of oral cilia.

Figure 8. *Diplodinium ecaudatum*. From Sharp (1914). ABBREVIATIONS *ador. m.* -- adoral membranelles. *an.* -- anus.*ant. cil. r.* -- anterior ciliary roots.*ant. c. v.* -- anterior contractile vacuole.*bd. l.* -- boundary layer (ectoplasmic).*cir. osa. r.* -- circumoesophageal ring.*caoc.* -- caocum.*cut.* -- cuticle.*c. v. r.* -- region about contractile vacuole.*D.* -- dorsal side of body.*d. disk* -- dorsal disk.*d. fur.* -- dorsal furrow.*d. m. str.* -- dorsal motor strand.*d. m.* -- dorsal membranelles.*ect.* -- ectoplasm.*ent.* -- entoplasm.*fd. vac.* -- food vacuoles.*i. ador. lip* -- inner adoral lip.*i. d. lip* -- inner dorsal lip.*L.* -- left side of body.*l. sk. a.* -- left skeletal area.*mac.* -- macronucleus.*mic.* -- micronucleus.*m. m.* -- motor mass (motorium).*o. ador.*

fur. -- outer adoral furrow. *o. ador. lip* -- outer adoral lip.*o. d. fur*. -- outer dorsal furrow.*o. d. lip* -- outer dorsal lip.*oes*. -- oesophagus or cytopharynx.*oes. f.* -- oesophageal fibers.*oes. retr. str*. -- oesophageal rectrator strands.*op*. -- operculum.*op. f.* -- opercular fibers.*or*. -- oral opening, mouth, or cytostome.*or. cil*. -- oral cilia.*or. disk* -- oral disk.*post. cil. r*. -- posterior ciliary roots.*post. c. v*. -- posterior contractile vacuole.*R*. -- right side of body.*rect*. -- rectum.*rect. f*. -- rectal fibers.*r. sk. a*. -- right skeletal area.*sk. lam*. -- skeletal laminae.*susp. f*. -- suspensory fibers.*V*. -- ventral side of body.*v*. and *r. sk. lam*. -- ventral and right skeletal laminae.*v. sk. a*. -- ventral skeletal area.*n. m*. -- nuclear membrane.

A remarkable example demonstrating preformation is presented by the ciliate protozoan *Diplodinium (Epidinium) ecaudatum* **(Figure 8)** which exists in huge numbers as symbionts in the stomachs of cattle. This tiny creature has a kind of "brain" (motorium)with circumoesophageal "nerve" connectives resembling those of annelids and arthropods, "muscles" (myonemes), a kind of segmental"spinal column" (skeletal laminae), a "mouth", "esophagus", "rectum"and "anus" (cytopyge), all elaborated within the confines of a single cell (Sharp 1914). Such an animal not only proves that all the necessary information is already present for these structures at the protozoan level, but at the same time it serves to cast serious doubt on the notion that multicellularity is a necessary prerequisite for the division of labor. Why this creature should have such an array of advanced features remains a complete mystery. Could it be there to provide us with a clue concerning the nature of the evolutionary process? I like to think so!

Another example is provided by the precocious evolution of the placenta in animals as primitive as certain sharks. Leo Berg (1969) discussed these and related phenomena at some length to provide examples of what he called *physiological acceleration*, an interpretation in obvious accord with the preformation concept.

More recently, the discovery of the homeobox gene complex has led to its identification in a great variety of living creatures. This too can be taken to support the notion that much of the necessary information for subsequent evolution is present very early with only a fraction of it being expressed in the evolution of a particular life form. A comparable phenomenon is apparent during ontogeny in which each cell in the body may contain all the information for the synthesis of every protein but only a small fraction of that information is expressed in a particular cell type, as for example, the synthesis of hemoglobin only in erythroblasts or pepsinogen only in certain cells of the stomach lining.

The very word evolution is derived from the Latin *evolvo*, meaning to unfold, as the pages of a book, thereby indicating that the information is already present (preformed).

On the other hand, epigenesis may be demonstrated in many evolutionary sequences. For example, with the evolutionary replacement of cartilage with bone, aquatic vertebrates acquired a density greater than that of water and would have been relegated to the bottom were it not for the invention of the swim bladder, a hollow outgrowth of the embryonic digestive system. This hydrostatic organ is homologous with the lung which, of course in turn, made the invasion of land possible and ultimately the evolution of the higher vertebrate taxa (amphibians, reptiles, birds and mammals).

On the other hand, the continuing success of the Chondrichthyes (sharks, skates, rays and chimeras) may reside in their having remained cartilaginous, and accordingly less specialized, and thereby less prone to extinction. It should also be mentioned that when a structure is lost during evolution it is rarely restored. Returning to the previous example, the darters, tiny members of the perch family of fishes, have lost the swim bladder, a loss which allowed them to invade swiftly flowing freshwater streams. This example also can serve to offer an alternative view to what the Darwinians would regard as an adaptation to the swift stream environment. Isn't it possible that the darters, having lost the swim bladder, stumbled into the stream environment or perhaps even sought it out? Admittedly this loss can be regarded as adaptive but only with respect to that rather specialized environment. Also, are we to believe that the loss of the swim bladder was a gradual process as the Darwinian view would suggest? It would seem that a great many evolutionary changes have involved instantaneous specializations of one sort or another. This general tendency maybe yet another reason for extinction.

Leo Berg's early insight into these matters was truly awesome. He clearly recognized the role of preformation and epigenesis in both phylogeny (evolution) and ontogeny (development) and supported his convictions with a multitude of examples (Berg 1969). He was, in my estimation, a true evolutionary prophet.

VII-3. Ontogeny and phylogeny compared

The present contains nothing more than the past, and what is found in the effect was already in the cause. -- Henri Bergson. *According to Darwinian doctrine and Crick's central dogma, DNA is not only the depository and the distributor of the information but its* ***sole creator****. I do not believe this to be true.* -- Pierre Grassé

There is no question that all of the information necessary to produce a unique human being is contained in a single cell, the fertilized egg, a mere tenth of a millimeter in diameter. While the information is preformed, the development of the individual is largely epigenetic.

I now suggest that precisely the same relationship may exist with respect to phylogeny (evolution). Viewed in this manner, both development and evolution result from the organized and progressive activation (derepression) of an incredibly enormous storehouse of potentialities. I realize that this suggestion seems ludicrous at first sight when applied to the evolutionary process, yet I feel it is necessary as it can offer an explanation for a number of otherwise baffling realities. Of cardinal importance is the question -- Where did all the information come from? If, as is so obvious at the onset of ontogeny, the information were also present from the start of the evolutionary process, someone or something had to put it there. That same someone or something apparently produced the inanimate world with all its rules, laws and precise mathematical relationships.

It is my understanding that information does not arise *de novo*, but must have a source. In that sense I agree with Grassé as quoted above.

It should also be noted that Schindewolf, Goldschmidt, Berg and Grasséall subscribed to preadaptation during evolution, a consideration that demands the presence of meaningful information prepared in advance, *i.e.* preformed. These conclusions are nothing more than the extrapolation to the living world of Albert Einstein's conviction -- "I shall never believe that God plays dice with the world."

Once again, I insist that the only alternative to chance is design, which in turn implies purpose. Let me also add that I fail to see how this perspective can in any way interfere with the search for ultimate truth. On the contrary, I have come to regard it as a liberating asset in that endeavor!

There is an entirely different reason to take this suggestion seriously. It can offer insights into a number of otherwise enigmatic observations from comparative biology. Two of these have already been mentioned: the presence of a placenta in certain sharks and the remarkable ciliate protozoan *Diplodinium ecaudatum* **(Figure 8)**.

The Onycophoran worm *Peripatus,* with its strange combination of arthropod and annelid characters, can seem perfectly reasonable from this perspective. Incidentally, *Peripatus* also nourishes its developing embryos with a kind of placenta as was noted by Berg (1969). Thus, *Peripatus* combines features of three different taxa: Annelida, Arthropoda and the placental Mammalia.

The primitive chordate Amphioxus (*Branchiostoma lanceolatus*), while it has all three chordate structures (gill slits, a dorsal hollow nervous system and a notochord), possesses a kidney consisting of solenocytes of the protonephridial (flame cell) type characteristic of the Platyhelminthes (flatworms), the Aschelminthes (roundworms) and the polychaete Annelida, none of which could possibly be regarded as its close relative.

On the other hand, certain oligochaeteannelids (earthworms) have a tubular kidney system more like that of vertebrates. The Apoda (limbless amphibians) have large yolk-laden eggs suspended by albuminous chalazae closely resembling the situation in the cleidoic (shelled) eggs of reptiles and birds. They lack only the calcareous shell. Other strange evolutionary puzzles such as the egg-laying monotreme mammals (the Platypus and the Echidna) are commonplace in comparative zoology, yet can suddenly become reasonable within the preformation context. When it comes to the possible combinations of characteristics one can almost say -- Anything goes!

The plant kingdom abounds with similar examples such as the occurrence of distantly related plant species producing similar, if not chemically identical, flavors of lemon, orange, anise, apple, pineapple, cinnamon and a host of other pleasant aromas so valuable to our cuisine. They may simply have drawn from the same common storehouse of available information.

The morphological similarities which exist between the Orthopteran leaf and stick insects (Phasmodea) and the plants which they inhabit acquire simple explanations in this light. Berg (1969) noted that the eggs of one of these insects (*Phyllium crurifolium*) closely resemble, both internally and externally, the seeds of the plants (Umbelliferae) with which it is commonly associated and, like the seeds, are scattered on the ground where they may remain for up to two years. These symbioses need no longer seem baffling if one simply assumes that the informational potential was available to both the plant and animal kingdoms when those evolutionary events occurred.

A similar argument would apply to the origins of the structural and behavioral reciprocities that often exist between flowers and their insect pollinators. As another example, the tunic of the sea squirts (Urochordata) is composed of cellulose, otherwise a plant product.

The list could go on and on.

Of course how all this was effected remains a total mystery, but this perspective at least avoids assuming a Lamarckian mechanism for which no evidence has been forthcoming. Similarly, the whole phenomenon which has been described as convergent evolution cannow take on an entirely new significance as the selection of very similar morphologies drawn from a universal stockpile of preformed potentialities which were available when those evolutionary events took place. In other words, what has been described as convergent evolution is not really that at all, but rather an identity already established (preformed). Unfortunately, since evolution seems no longer to be in progress, we may never be able to directly observe such transformations.

VII-4. The rate of evolution

Now! Now! cried the Queen. Faster! Faster! -- Lewis Carroll

It is of interest to compare the predictive value of the Darwinian and semi-meiotic models with respect to evolutionary rates. The Darwinian view predicts long periods of gradual change with many intermediate forms. The semi-meiotic concept is the very antithesis, with new life forms being produced instantly as a result of the cytological events which occur during the first meiotic division in oocytes bearing one or more chromosome rearrangements in heterozygous form. As I indicated earlier, one half of the products of oocytes bearing a single heterozygous rearrangement will be like the original type and one half will be a new chromosome structural homozygote and, possibly, a new and discrete species. As improbable as this may seem at first glance, it is nevertheless precisely what the semi-meiotic hypothesis predicts -- namely, *instant speciation.* The time constants for this process would then be on the order of minutes, or even seconds, rather than the extensive periods of time required by the Darwinian model. This suggestion remains in complete agreement with Schindewolf's recommendation that we might as well stop looking for the missing links as they never existed.

I wholeheartedly agree!

The semi-meiotic hypothesis also puts the origin of *Homo sapiens* in a whole new perspective. Since we coexisted with and were preceded by Neanderthal man, isn't it possible that he (or rather she to be precise) was our instantaneous predecessor with no intermediates involved in the process? It would be fascinating to be able to reproduce the Neanderthal karyotype, as it could be an acid test of the semi-meiotic hypothesis. I suggest that the two karyotypes might differ only by one or a few structural rearrangements, perhaps only by a single homozygous inversion. I would also anticipate, for reasons already discussed, that the Y (male determining) chromosomes might prove to be quite dissimilar.

VII-5. Has evolution been guided?

I want to know God's thoughts ... the rest are details. -- Albert Einstein

The most beautiful thing we can experience is the mysterious. It is the source of all true Art and Science. -- Albert Einstein

Men despise religion. They hate it and are afraid it may be true. The cure for this is first to show that religion is not contrary to reason, but worthy of reverence and respect. -- Blaise Pascal

I am aware of the negative effect this query may have on certain members of the intellectual community. Nevertheless I feel it is a perfectly valid, and thereby a scientific, question since the role of chance is, to say the very least, questionable. This question is intimately related to the question -- Are there laws governing evolution? I realize that some distinguish between those laws that they regard as natural and those that they reject as being unnatural, mystical or otherwise unacceptable. I see no reason to make those distinctions. Laws are laws whether or not we like them or understand them. For example, everyone accepts the reality of gravitation and Galileo's equation relating the distance of falling objects to time. However, no one as yet understands the cause of gravity.

Thus, neither in religion nor in science does acceptance demand understanding. If not chance, it seems to me that the only rational alternative is that both evolution and development have indeed proceeded according to law just as Leo Berg has insisted. The only real unknown is the nature and purposes of the law maker or makers. Don't our representatives in congress usually have some purpose in mind when they enact legislation? Also, seriously considering the possibility of guidance may serve to ameliorate the unfortunate situation which continues to separate the religious and scientific communities.

Is it not possible that both perspectives might be correct? I have come to believe that it is and, in so doing, join with Albert Einstein: "Science without religion is lame, religion without science is blind”.

"I will address this issue first with the views of others and finally with a single apparent fact from the fossil record. Some of our greatest intellects have been physicists. In addition to Pascal, Galileo, Newton, Faraday and of course Einstein, among many others, all acknowledged God one way or another. More recently, Richard P. Feynman (1998) compared scientific discovery to a religious experience. L.C. Dunn (1965) pointed out that Mendel's data are so nearly ideal that his paper might be considered a demonstration, rather than a test, of the laws that now bear his name. It is fair to say that we still have not identified the source of bright ideas, insights and creative acts of genius. Mendel, as the abbot of his Augustinian monastery, at least serves as an example that one need not be an atheist to conduct first class research!

In contrast with the great physicists I have mentioned, why so many biologists remain professed atheists or agnostics is a complete mystery to me. Every aspect of both the living and nonliving worldis totally at odds with those positions. Nevertheless, the Darwinians continue to insist that all of evolution is the result of mere chance events. Stephen J. Gould has recently compared the evolutionary process to a drunk reeling back and forth between the bar room wall and the gutter (1996, page 149). He has also described intelligence as an "evolutionary accident". I will only say that it was *some* accident! Richard Dawkins' *Selfish Gene*, *Blind Watchmaker*, and *Climbing Mount Improbable* require no further comment from me.

When Alfred Russel Wallace first expressed his views they were essentially identical with those of Charles Darwin. The question arises whether Darwin would ever have published the *Origin* had it not been for Wallace. We do know that Darwin had entertained the mechanism of natural selection for several years and that he was urged by his friends to publish in order to establish priority.

The important point here is the way in which these two naturalists subsequently came to differ in their interpretation of the evolutionary process. While Darwin remained steadfast, Wallace underwent at first a partial and then a complete intellectual metamorphosis which is obvious from the complete title of his last book -- *The World of Life: A Manifestation of Creative Power, Directive Mind and Ultimate Purpose* (1911).

I quote from the penultimate paragraph of his Preface because it reflects precisely my own feelings with respect to the semi-meiotic hypothesis. I also wish to point out that, however strange and heretical some of my beliefs and suggestions seem to be, I claim that they have only been arrived at by a careful study of the facts and conditions of the problem. I now offer but a single observation that bears on the question of whether or not evolution has been guided. It relates to Robert Broom's opinion that not a single new genus has appeared in the last two million years. It would seem that the last genus was *Homo* and the last species *Homo sapiens*.

I rest my case.

VIII. Conclusion

Facts which at first seem improbable will, even on scant explanation, drop the cloak which has hidden them and stand forth in naked and simple beauty. – Galileo *No biologist worthy of his reputation can limit himself to criticism of accepted doctrine, however necessary and valuable it may be; he has to construct, and is able to do so if he can discard accepted ideas and view evolutionary phenomena from new angles inthe light of recent advances in paleontology and molecular biology*. -- Pierre Grassé

It is in the spirit of the above quotation from Grassé's book (1977) that I have presented this material. The most convincing thing in favor of the Semi-meiotic hypothesis is the independence with which so many virtually identical conclusions have been reached by so many of my distinguished predecessors.

For example, Grassé (1977) made no mention of Broom, Huxley and Petrunkevitch but reached the same conclusion that evolution is largely finished and has been for millions of years. Similarly, Broom and Schindewolf independently reached the conclusion that the individual is the unit of evolutionary change. Berg reached the same conclusion as Punnett, Osborn and Bateson that the role of selection is to prevent change rather than to produce it, a conclusion also reached by Grassé (1977, page 119). Goldschmidt, Schindewolf and Berg all concluded that saltation is the mechanism for all significant (trans-specific) evolutionary change. Both Grassé and Berg emphasized internal (endogenous) factors as of great evolutionary significance yet neither mentioned the other.

Grassé and Schindewolf both maintained that evolution is irreversible. Luther Burbank and William Bateson each independently questioned the capacity of sexual reproduction to support evolutionary change. These were not mere coincidences but reasoned conclusions reached after a careful consideration of all the facts which were then available.

None of this can be accommodated within the Darwinian model. We owe these men a great debt. Referring back to Robert Burton whom I quoted in the dedication, let me say that I am the dwarf standing on the shoulders of these great investigators. It will be with a sense of great personal satisfaction if I am able to help place these scholars in their rightful and long overdue positions as enlightened pioneers in the exploration and clarification of the great mystery of evolution. Every shred of tangible evidence points to sexual reproduction as a highly conservative device, serving only to bring evolution to a virtual standstill. Just as William Bateson indicated even before 1900, I too find it amazing how long the Darwinian view has prevailedin the face of an enormous and continually growing body of information with which it cannot possibly be reconciled.

In short, Darwinism must be abandoned as a meaningful instrument of organic change. I realize that paradigms are expected to be replaced before they are discarded. It is with that end in mind that I have continued to pursue the Semi-meiotic hypothesis. I have time and again tried to discredit it and have failed. I invite others to attempt the same.

Let me also add that I cannot conceive of any other device that could have operated to produce the sort of evolutionary changes that we know have taken place. Furthermore, the Semi-meiotic hypothesis remains in complete accord with all that I have been able to glean from the experimental and descriptive literature in embryology, cytology, paleontology, taxonomy, comparative and general anatomy, comparative and general physiology, biochemistry and genetics.

A second consideration has to do with the nature of the scientific method. Scientists have traditionally relied on experiment to discover the truth. Embryology, Biochemistry, Physiology and Genetics all have progressed through experiment. Where is Experimental Evolution? I submit that in the past there was great interest in Experimental Evolution, but since the findings were largely negative they were not published. In all fairness, I must acknowledge that Schindewolf was steadfastly opposed to the idea of Experimental Evolution and maintained that it cannot be investigated in that way (1993, page 311). I remain unconvinced that he was correct on this most critical point.

The Semi-meiotic hypothesis is eminently testable in suitable material. I am optimistic that this hypothesis may offer an experimental opportunity to provide insight simultaneously into the two greatest unsolved problems in all of biological science, the other being the mystery of embryonic development. The two are unquestionably intimately related just as Leo Berg so clearly recognized long ago.

Thus, while evolution may or may not be finished, I remain hopeful that we have the capacity to produce new and hitherto unknown higher life forms (true species or perhaps even higher taxonomic categories) in the laboratory. I predict that this goal may be realized through the experimental inhibition of the second meiotic division in female animals that either are heterozygous for chromosome structural rearrangements or that bear oogonia that are. Experiments to realize that end are in progress.

To slightly modify an old adage: "*God works in mysterious (semi-meiotic) ways*."

REFERENCES

ANDREWS, P. (1987) Aspects of hominid phylogeny. In: Colin Patterson (ed.), *Molecules and Morphology in Evolution. Conflict or Compromise?* Cambridge University Press, Cambridge.

BATESON, W. (1894) *Materials for the Study of Variation*. Macmillan and Co., New York.

BATESON, W. (1913) *Problems of Genetics*. Yale University Press, Cambridge. BERG, L. (1969) *Nomogenesis; or, Evolution Determined by Law*. M.I.T. Press, Cambridge. (Original Russian edition 1922.)

BROOM, R. (1932) Evolution as the paleontologist sees it. *South African Journal of Science*, 29: 54-71.

BROOM, R. (1933) Evolution -- Is there intelligence behind it? *South African Journal of Science*, 30: 1-19.

BROOM, R. (1933) *The Coming of Man*. H.F. and G. Witherby, London.

BROOM, R. (1951) *Finding the Missing Link*. Watts, London.

BULL, J.J. (1983) *Evolution of Sex Determining Mechanisms*. Benjamin Cummings, Menlo Park.

BURBANK, L. (1939) *Partner of Nature*. D. Appleton-Century Co., New York.

CLEVELAND, L.R. (1947) The origin and evolution of meiosis. *Science*, 105: 287-289.

DARWIN, C. (1896) *The Origin of Species by Means of Natural Selection*. D. Appleton, New York.

DAVISON, J.A. (1961) A study of spotting patterns in the leopard frog. 1. Effect of gene dosage. *J. Heredity*, 52: 301-304.

DAVISON, J.A. (1984) Semi-meiosis as an evolutionary mechanism. *J. Theor. Biol.*, 111: 725-735.

DAVISON, J.A. (1987) Semi-meiosis and evolution: a response. *J. Theor. Biol.*, 126: 379-381.

DAVISON, J.A. (1993) The blind alley: Its significance forevolutionary theory. *Rivista di Biologia (Biology Forum)*, 86: 101-110.

DAVISON, J.A. (1998) Evolution as a self-limiting process. *Rivista di Biologia (Biology Forum)*, 91: 199-220.

DAWKINS, R. (1976) *The Selfish Gene*. Oxford University Press.

DAWKINS, R. (1986) *The Blind Watchmaker*. W.W. Norton, New York.

DAWKINS, R. (1996) *Climbing Mount Improbable*. W.W. Norton, New York.

DUNN, L.C. (1965) *A Short History of Genetics: The Development of Someof the Main Lines of Thought, 1864-1939*. McGraw-Hill, New York.

FEYNMAN, R.P. (1998) *The Meaning of It All: Thoughts of a Citizen Scientist*. Addison-Wesley, Reading, Massachusetts.

GOLDSCHMIDT, R.B. (1940) *The Material Basis of Evolution*.Yale University Press, New Haven.

GOULD, S.J. (1996) *Full House: The Spread of Excellence from Plato to Darwin*. Harmony Books, New York.

GRANT, P.R. & GRANT, B.R. (1994) Phenotypic and genetic effects of hybridization in Darwin's finches. *Evolution*, 48: 297-316.

GRASSÉ, P. (1977) *Evolution of Living Organisms: Evidence for a New Theory of Transformation*. Academic Press, New York. (Original French edition 1973.)

HUXLEY, J. (1942) *Evolution: The Modern Synthesis*. Harper, New York and London.
KOESTLER, A. (1971) *The Case of the Midwife Toad*. Random House, New York.
LINDSLEY, D.L., FANKHAUSER, G. & HUMPHREY, R.R. (1956)Mapping centromeres in the axolotl. *Genetics*, 41: 38-64.
MAYR, E. (1982) *The Growth of Biological Thought*. Harvard University Press, Cambridge, Massachusetts.
NACE, G.W. & RICHARDS, C.M. (1969) Development of biologically defined strains of amphibians. In: Merle Mizell (ed.), *Biologyof Amphibian Tumors*. Springer-Verlag, New York-Heidelberg-Berlin.
NIEUWKOOP, P.D. & SUTASURYA, L.A. (1979) *Primordial Germ Cells in the Chordates*. Cambridge Univ. Press, Cambridge.
OLSEN, M.W. (1961) Segregation and replication of chromosomes in turkey parthenogenesis. *Nature*, 212: 435-436.
PETRUNKEVITCH, A. (1952) Macroevolution and the fossil record of Arachnida. *Amer. Sci*., 40: 99-122.
PUNNETT, R.C. (1915) *Mimicry in Butterflies*. University Press, Cambridge.
SCHINDEWOLF, O. (1993) *Basic questions in Paleontology*. University of Chicago Press, Chicago. (Original German edition 1950.)
SHARP, R.G. (1914) Diplodinium ecaudatum, with an account of its neuromotor apparatus. *University of California Publications in Zoology*, 13: 43-123.
VORONTSOV, N.N. (1973) The evolution of the sex chromosomes. In: A.B. Chiarelli & E. Capanna (eds.), *Cytotaxonomy and Vertebrate Evolution*. Academic Press, New York.
WALLACE, A.R. (1911) *The World of Life; A Manifestation of Creative Power, Directive Mind and Ultimate Purpose*.Moffat Yard and Co., New York.
WEISMANN, A. (1891) *Essays upon Heredity and Kindred Biological Problems*. Clarendon Press, Oxford.
WHITE, M.J.D. (1973) *Animal Cytology and Evolution*. Comstock Publ. Co., Ithaca, New York.
WILSON, E.B. (1925) *The Cell in Development and Heredity*. Macmillan, New York.

WINGE, O. (1950) *Inheritance in Dogs: with Special Reference to Hunting Breeds*. Comstock Publ. Co., Ithaca, New York.
WITSCHI, E (1956) *Development of Vertebrates*.W.B. Saunders, Philadelphia.
YUNIS, J.J. & PRAKASH, O. (1982) The origin of man: A chromosomal pictorial legacy. *Science*, 215: 1525-1530.