

"The Blind Alley: Its Significance for Evolutionary Theory"

John Davison writes as follows:

"Several scientists have apparently independently used the term "Blind Alley" to indicate that major evolutionary change has ceased."

He continues with the following two quotations.

"Evolution is thus seen as a series of 'Blind Alleys'. 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"(HUXLEY 1963).

"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 been evolved since the Eocene. All major evolution has apparently come to an end. No new types of fishes, no new 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" (BROOM 1951).

THE "BLIND ALLEY": ITS SIGNIFICANCE FOR EVOLUTIONARY THEORY

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Abstract

Several scientists have apparently independently used the term "Blind Alley" to indicate that major evolutionary change has ceased. The failure to observe speciation through selection would indicate that obligatory sexual reproduction is incapable of producing progressive evolution. Favoring this conclusion is the evidence that sex determination has independently evolved and may be further correlated with the equally nonhomologous evolution of contemporary gametic sources in the same animal groups. To incorporate these facts into a meaningful theory demands the postulate of a presexual mode of reproduction which has been suggested as identical with the first meiotic division. A hypothetical scenario for macroevolution is presented.

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Has Evolution Come To An End?

In reviewing the evolution literature I was struck by the occurrence of the words "blind alley" when various authors were discussing the evolutionary process. Once having identified the cause of the blind alley I will follow that identification to its logical conclusions for our understanding of the evolutionary process. Except for generic names, all italics have been added by me.

I begin with Julian Huxley, one of a group of biologists including Mayr, Stebbins, Dobzhansky, Wright and Simpson, who collectively instituted what they called the "Modern Synthesis." This was, in effect, a consensus that evolution was essentially a neo-Darwinian process emphasizing isolation and natural selection as creative forces in the molding of new life forms. In 1942 Huxley summarized the literature in his book appropriately titled "Evolution: The Modern Synthesis". The so-called second edition, published in 1963 is actually the eighth printing of the 1942 text. On page 571, seven pages from the end, Huxley presents the following revealing summary.

"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"(HUXLEY 1963).

Huxley was not alone in these conclusions. Compare his views with those of the anti-Darwinian paleontologist Robert Broom.

"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 been evolved since the Eocene. All major evolution has apparently come to an end. No new types of fishes, no new 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" (BROOM 1951).

In an earlier work Broom was more explicit.

"There is, however, no doubt that evolution, so far as new groups are concerned, is at an end. That a line of small generalized animals should have continued on till in Eocene times the Primates originated and then ceased, and that except for specialisations 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, ..." (BROOM 1933).

If one accepts the notion that macroevolution involves the formation of new kinds (genera) of living things, then Broom is saying that all macroevolution ceased about two million years ago.

Sexual Reproduction As The "Blind Alley"

Now for the question: If, as these authors have indicated, major evolutionary change has indeed ceased, what caused the process to come to a halt? In probing for an answer to this question I consulted the opinions of one whose entire career involved the alteration of living things through intensive artificial selection. While he does not use the term "Blind Alley" his conclusions imply as much. From his autobiography Luther Burbank writes:

"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 grape-fruit. I have daisies on my farms 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..... In short, there are limits to the developments possible, and these limits follow a law" (BURBANK 1939).

Notice that Burbank does not even consider the question of speciation, rather he indicates with confidence the limited extent within the species to which selection can go, essentially endorsing the "Blind Alley" position. This I found rather remarkable since Burbank, who was rather indifferent towards Mendelism, was an enthusiastic Darwinian (BURBANK 1931).

In this regard it is useful to recall the final words in Darwin's Origin of Species

"...endless forms most beautiful and most wondrous have been and are being evolved" (DARWIN 1896).

While no serious scientist questions the evidence that evolution has occurred, I hope the foregoing may serve to justify asking whether or not it is still occurring. More specifically the question might be phrased - can diploid, sexually-reproducing organisms undergo evolutionary change?

Darwin relied heavily on the variation observed among litter mates as the source of differences upon which natural selection could act. With the rediscovery of Mendelian genetics in 1900 a great impetus was given to Darwinism as a source of variation was finally revealed - the particulate gene. A chief exponent of the new science of genetics was William Bateson, properly regarded as the father of modern genetics. He coined the terms genetics, allelomorph, dominant, recessive and Mendelism (DUNN 1965). His enthusiasm for Mendelism apparently extended to naming his son Gregory when he was born in 1903. William Bateson was the earliest of my sources to use the term "Blind Alley" and it is of interest to recognize how this comment came to be revealed.

In 1970 Arthur Koestler was completing research on his book "The Case of the Midwife Toad", dealing with the career of the Lamarckian zoologist Paul Kammerer. His research included an interview in June 1970 with Bateson's son Gregory, who offered the following recollection to Koestler:

"By 1924, Bateson had come to realize, and told his son in confidence, 'that it was a mistake to have committed his life to Mendelism, that it was a blind alley which would not throw any light on the differentiation of species, nor on evolution in general'" (KOESTLER 1971).

Mendelism is of course the genetics associated with sexual reproduction. Bateson seems to be saying the same thing that Burbank is saying, i.e. sexual forms are incapable of progressive change. The obvious inference is that sexual reproduction is the "Blind Alley" of evolution. This consideration forces another question. Is there another kind of genetics other than the Mendelian variety? It is again useful to review the historical record.

Chromosome Repatterning and Macroevolution

The publication of R. B. Goldschmidt's "The Material Basis of Evolution" in 1940 marks a pivotal point in the history of evolutionary thought. The text is in two sections, microevolution and macroevolution. The first section on microevolution ends with this statement so 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 that of sheer accumulation of micromutations" (GOLDSCHMIDT 1940).

This view was echoed a decade later by the systematist Petrunkevitch (PETRUNKEVITCH 1952).

"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 Diptera were completed in the comparatively distant past... At any rate it seems imperative that the methods for the production of viable 'hopeful monsters' should be different from those employed for the production of microevolutionary changes."

This call for a different evolutionary method should not be taken lightly. Like any new method two aspects present themselves. The first is the method itself, the second, the means by which the method has been implemented.

The other method to which Goldschmidt refers is the reorganization of existing genetic information within the structure of the chromosome, a phenomenon loosely defined as position effect. In his words

"... 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" (GOLDSCHMIDT 1940).

Unfortunately, Goldschmidt's views were not taken seriously at the time. First, the authors of the "Modern Synthesis" were in the process of collectively stating their case for neo-Darwinism and simply chose to ignore Goldschmidt's challenge. Second, molecular biology was emerging and emphasis on the more traditional methods of cytogenetics was being overshadowed by interest in the biochemistry of the nucleic acids and the emergence of the genic control of enzyme synthesis.

In any event we now know that Goldschmidt was prophetic indeed. Modern staining techniques allow us to visualize chromosomal repatterning in a wide variety of life forms including the higher primates which serve as a good example of what might be called position effect genetics.

While DNA hybridizing techniques (ANDREWS 1987) have revealed a surprising degree of similarity between ourselves and our close relatives, the one clear distinction between us is that foreseen by Goldschmidt. The 1982 paper by Yunis and Prakash (YUNIS and PRAKASH 1982) illustrates that the major differences between ourselves, chimpanzees, gorillas and orang-utans are evidenced as a repatterning of what seems to be otherwise identical blocks of euchromatic chromosomal information. The notion of the chromosome as a field of reaction, considered radical in Goldschmidt's day, is now accepted in the cytogenetics literature along with a renewed interest in position effect genetics (LIMA-DE-FARIA 1983).

The Nonhomology of Both Gamete Origins and Sex-Determination

I now come to the question of how these new patterns came to be. If Burbank, Bateson and the others are correct in their assessment of the limitations of sexual reproduction, then it follows that macroevolution would be expected to involve a presexual mode of reproduction. It further follows that sex-determining mechanisms would be expected to evolve independently in various plant and animal groups. Such is apparently the case. All known mammals have male heterogamety with the familiar XY male and XX female. By contrast, all birds are the opposite with ZW females and ZZ males. A similar dichotomy apparently evolved within the amphibia with most urodeles (newts and salamanders) like birds and all anurans (frogs and toads) except *Xenopus* like mammals. In reptiles examples of both kinds occur as well as temperature determination of sex in certain turtles and crocodylians.

Among the arthropods similar differences prevail. Diptera generally have heterogametic males while Lepidoptera are like birds and urodeles with heterogametic females. In the social insects a haplo-diplo (male-female) system operates. In certain parasitic forms even the size of the host can determine the sex of the parasite. The literature is well reviewed in Bull's (BULL 1983) book significantly titled "Evolution of Sex Determining Mechanisms". The Russian

cytologist N. N. Vorontsov was one of the first to call attention to the nonhomology of the various sex determining devices.

"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 Insecta and Mammalia, whereas the ZW-ZZ system evolved independently in Trichoptera, Lepidoptera, Serpentes and in 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" (VORONTSOV 1973).

This remarkable conclusion is of course totally incompatible with the neo-Darwinian concept of the evolutionary process.

It is again useful to recall the historical literature. August Weismann (WEISMANN 1891) was one of Darwin's most ardent supporters and was instrumental in ridding Darwinism of its Lamarckian elements, leading to what we now regard as neo-Darwinism. He popularized the idea of the continuity of the germ plasm with all heritable changes originating in the reproductive cells. The notion of the continuity of the germ cells seems so reasonable that it might never occur to someone that it might not be so, yet that is exactly what a large body of experimental and descriptive literature clearly discloses.

I have discussed this evidence elsewhere (DAVISON 1984) and will simply summarize the salient features for the purpose of the present argument.

The vertebrate gonad develops from portions of the urogenital ridge, a bipartite structure consisting of an outer cortex and inner medulla. The gonadal cortex develops into the ovary, the medulla into the testis. Oddly the vertebrate gonad is a sterile organ completely incapable of functioning as a germinal epithelium (NIEUWKOOP and SUTASURYA 1979). During embryonic development the gonad receives, by a process of invasion, presumptive germ cells from extra-gonadal sources. Gonads failing to receive these cells remain sterile, while those receiving presumptive germ cells differentiate with the sex of the host organ not that of the donor cells. Thus the gonad proper is clearly a part of what Weismann called the somatoplasm.

The important point to make here is that the sources as well as the means of induction and modes of reaching the gonad vary in nonhomologous fashion from vertebrate group to group in a manner which remarkably parallels the equally nonhomologous modes of sex determination.

In mammals, including man, the presumptive germ cells are first seen in the region of the allantois corresponding roughly to the position of the urinary bladder in the adult. From here they migrate anteriorly and laterally to enter the embryonic gonad. In birds the future germ cells originate outside the embryonic axis in the extra-embryonic endoderm consisting of the so-called germinal crescent anterior and lateral to the head. From here they enter the vitelline circulation and after a period in the circulatory system invade the gonad after first passing through the walls of the venous circulation. Reptiles, as one might expect, show a similarity with

variations on the bird mechanism. It is in the amphibia that the most dramatic differences are manifest in the origin of the germ cells. From their monograph Nieuwkoop and Sutasurya write:

"When comparing PGC formation in the urodeles with that in the anurans, one is unavoidably led to the conclusion that not only do the PGCs originate from two different sites in the two groups, but that there are moreover two fundamentally different mechanisms at work ... In the anurans all the PGCs originate from the endodermal moiety of the egg in the vicinity of the vegetal pole, whereas in the urodeles they arise from the animal 'ectodermal' moiety, more particularly the presumptive lateral plate mesoderm in the ventral to ventro-lateral equatorial region. In the anurans all the descriptive and experimental evidence pleads in favor of the predetermined nature of the PGCs, based on the presence of a germ-cell-specific cytoplasmic component, the germinal plasm, which is present in the embryo from the very beginning of development. In contrast, in the urodeles the PGCs develop strictly epigenetically from common, totipotent cells of the animal moiety under the inductive influence of the ventral yolk endoderm" (NIEUWKOOP and SUTASURYA 1979).

Note the clear correlations between nonhomologous modes of sex determination and equally nonhomologous methods and sources for germ cell formation. As I have indicated elsewhere any theory of evolution must include in its postulates these fundamental differences (DAVISON 1984). As well as I can determine the neo-Lamarckians, the neo-Darwinians, and the Creationists all fail even to acknowledge the existence of this experimental and descriptive literature, not to mention its significance for their particular views. In that respect the Creationists are missing an opportunity for their case since nonhomology means separate origin, which prima facie might be interpreted to mean special creation.

Macroevolution As A Semi-Meiotic Process

To avoid that conclusion I prefer to approach the problem as follows.

First, since the definitive sex cells of the various vertebrate groups cannot be homologized, they cannot be considered as ancestral cell lineages. Rather they are secondary or derived lineages correlated in their origins with the equally independent and nonhomologous invention of sexual reproduction.

We may never know the original source of the reproductive cells but it may have been the gonad itself, since in the most primitive of the chordates, the tunicates and the cephalochordates (Amphioxus) the gonad apparently does still function as a germinal epithelium (NIEUWKOOP and SUTASURYA 1979).

Secondly, if the original source has been replaced, it seems reasonable that three phases may be postulated for the evolutionary scenario.

The first phase would be the pre-sexual phase employing the original and common source of reproductive cells, with these possibly derived from the gonad proper. I have suggested earlier that this form of pre-sexual reproduction could be a form cytogenetically the same as the first meiotic division. It should be recalled that the first meiotic division represents a perfectly valid form of diploid

reproduction in its own right, and has intrinsic in its chromosomal mechanism the capacity to produce from single chromosomal rearrangements those rearrangements as paired homozygotes in a single step, at the same time that it retains the original karyotype (DAVISON 1984). This is due of course to the universal property of the first meiotic division that the sister strands remain together. Such a cytogenetic system can go a long way toward explaining the absence of intermediate forms in the fossil record, since the original karyotype can go on producing gene rearrangements until a trial balloon suddenly results in a saltational evolutionary event. This phase would of course be exclusively female (gynogenetic) and as such would have a reproductive efficiency twice that of a typical sexual system. In a primitive world in which new niches are as yet unoccupied such a mode might be ideally suited for the implementation of major evolutionary inventions such as hair, feathers, cleidic eggs and other structural elements for which intermediates are extremely difficult to imagine. In addition to retaining the original wild type, the semi-meiotic model also serves to eliminate from the germinal line deleterious genes and gene arrangements since, except for crossing-over, these would be also expressed immediately as paired homozygotes (DAVISON 1987).

With the introduction of the extra-gonadal and sexual cell lineage, it seems to me that the two cell lineages would co-exist during the second phase of the evolutionary process. This phase would correspond to the explosive phases of mammalian and avian evolution already described by Huxley and Broom. The competition between the two reproductive devices could lead as it apparently has to the elimination of the primary semi-meiotic device, perhaps due simply to the capacity of the familiar sexual reproductive mode to fine-tune the genetic makeup to a relatively unchanging environment.

Sexual Reproduction As An Anti-Evolutionary Mechanism

Viewed in this way the role of sexual reproduction becomes one of evolutionary conservatism rather than evolutionary creativity, a function which serves to prevent rather than promote progressive change. Also, unlike the semi-meiotic model, sexual reproduction is not well suited to the elimination of deleterious genes and gene arrangements. The accumulation of such deleterious factors coupled with an innate inability to respond effectively to a rapidly changing environment may have been, in both past and present, important reasons for the extinctions which have characterized the record of life on the earth.

Also, if this interpretation is essentially correct, we should not be so quick to condemn Lamarckian evolution, since the properties of the original reproductive lineage are of course completely unknown. It is perfectly conceivable that those cells could respond to environmental agencies, which could serve as another reason for their elimination once a new adaptive plateau had been reached.

When the semi-meiotic hypothesis was first proposed (DAVISON 1984) I pointed out that it has yet to be demonstrated that any creature reproducing by obligatory sexual means is capable of evolution beyond the generic level. No

response to that challenge has been forthcoming and so I repeat the proposition. I hope the present paper will serve to stimulate a lively response from the community of evolutionists.

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