

## **Semi-Meiosis as an Evolutionary Mechanism**

JOHN A. DAVISON

*Department of Zoology, University of Vermont, Burlington,  
Vermont 05405-0086, U.S.A.*

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The definitive germ cells in various vertebrate classes do not arise from homologous sites. Correlated with these nonhomologies are non-homologous mechanisms of sex determination indicating that sexual reproduction has independently evolved in the animal kingdom. A presexual mode of reproduction is proposed consisting of a semi-meiotic mechanism involving only the first meiotic division. This mechanism is admirably suited to the mandatory production of gene rearrangements as paired homologues in a single step. Indirect and direct evidence for the semi-meiotic mechanism is presented as well as a hypothetical scenario for macroevolution.

### **Introduction**

Two of the most influential figures of nineteenth century biology were Charles Darwin (1871), with his theory of evolution through gradual change and August Weismann (1889), with his theory of the continuity of the germplasm. Weismann, younger than Darwin, saw in his own views a vehicle for the evolutionary changes Darwin proposed, namely, that any change in the body or somatoplasm must be preceded by a change in the reproductive cells or germplasm. He conceived of the germinal lineage as an immortal line extending back through time with the somatoplasm serving as a temporary and mortal structure for the purpose of ensuring reproductive continuity. Weismann's concept was neatly summarized by Samuel Butler: "A hen is only an egg's way of making another egg". An earlier figure, the geologist Charles Lyell (1868), influenced both Weismann and Darwin with his doctrine, which he called the principle of uniformity: the forces which we now see shaping the surface of the earth are the same forces which have operated in the past. Lyell's principle could only mean that the earth was very old, which in turn meant that plenty of time had been available for the evolutionary changes postulated by Darwin to have occurred. Thus Lyell's principle of uniformity, Weismann's continuity of the germplasm and Darwin's theory of evolution all meshed together to provide a beautifully logical mechanism for organic change.

Biological processes, unlike the geological processes studied by Lyell, are frequently self-limiting. Thus, a multicellular organism grows to adult size and then stops growing, much as embryonic cells stop differentiating once the differentiated state has been reached. It occurred to me that the evolutionary process might also be self-limiting. If that should be the case, one might anticipate that contemporary reproductive mechanisms would be different from those which operated during a period of active evolutionary change. Such differences, if demonstrable, could be interpreted as a violation of the principle of evolutionary uniformity and as support for the principle of evolutionary self-limitation. It is the purpose of this essay to present evidence for reproductive nonuniformity from the discipline of comparative embryology, a field which has been largely neglected by students of evolution. After presenting that evidence I will discuss correlative information from studies of sex determination and chromosome structure. Finally I will offer a mechanism for evolution which is compatible with the evidence I present.

### **The Nonhomologous Nature of the Contemporary Germ Cells**

The discipline of comparative anatomy has been indispensable in establishing the evolutionary affinities of various groups especially in the vertebrates. In doing so it has relied heavily on the evidence from comparative embryology. Thus to establish that certain structures are homologous (e.g. the lungs of tetrapods and the swim bladder of fishes), it is essential to demonstrate that these organs share a common origin. In this case each originates as a hollow outgrowth of the archenteron and accordingly the homology of these organs is established. Homology is also supported in the origin of the vertebrate gonad, which with minor variations always arises from portions of the urogenital ridges, bilateral longitudinal structures in the dorsolateral coelomic mesoderm of the vertebrate embryo. Curiously, however, the vertebrate gonad does not serve as a germinal epithelium itself but receives the presumptive germ cells by a process of invasion from sites elsewhere in the embryonic body. Nieuwkoop & Sutasurya (1979, 1981), have recently published two monographs summarizing the origins of the germ cells in chordates and invertebrates.

In the anuran amphibians (frogs and toads) the primordial germ cells (PGCs) are found after gastrulation in the dorsal medial endoderm of the archenteron from which site they migrate dorsally and laterally to enter the presumptive gonad. By contrast, in the urodeles (newts and salamanders) the PGCs first appear in the lateral plate mesoderm lateral to the urogenital ridges. From these bilateral sites the PGCs migrate in a medial direction

to populate the developing gonad. Summarizing the situation in amphibians, Nieuwkoop & Sutasurya (1979, p. 91) have this to say:

“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.” (Italics are mine.)

The situation in birds is entirely different from each of these amphibian groups. In birds the PGCs first appear in the extra-embryonic endoderm anterior and lateral to the head of the embryo, a region described as the germinal crescent. From this site they enter the circulatory system which carries them throughout the body of the embryo. In the vicinity of the gonad they exit the circulatory system and migrate into the gonad (Nieuwkoop & Sutasurya, 1979).

In the reptiles three distinct patterns of origin have been described. In *Sphenodon*, a primitive reptile, the PGCs are first seen in an extra-embryonic germinal ring completely encircling the embryo. In the Chelonia (turtles) the germinal crescent is posterior to the embryonic axis. Among the lizards, some have an anterior germinal crescent like the birds, others a posterior germinal crescent like the turtles (Nieuwkoop & Sutasurya, 1979).

In mammals, including man, the PGCs are first evident in the yolk sack closely associated with the developing allantois, a structure destined to become the urinary bladder in the adult. They reach the gonads by amoeboid migration through the dorsal mesentery (Nieuwkoop & Sutasurya, 1979).

After reviewing the literature concerning germ cell formation in the vertebrates and invertebrates, Nieuwkoop & Sutasurya (1981, p. 176) present the following general conclusion concerning the germ line concept:

“Taking all these arguments together we cannot avoid the conclusion that the fundamental distinction between *germen* and *soma*, implying the postulate of an uninterrupted germ line extending from one generation to the next, is no longer adequate and valid, since it is no longer supported by our present insight into germ cell development. We believe that it is time for this obsolete concept

to be abandoned and to be replaced by the idea that germ cell formation represents just another type of cellular differentiation."

It is not necessary to abandon Weismann's concept of continuity since the available evidence can be interpreted in an entirely different light. It is transparent that the germinal lineages I have discussed are simply not homologous with one another, even when the comparisons are made between urodeles and anurans, members of the same vertebrate class. Conservation of the principle of homology demands that there must have been a time during the evolutionary process when the germinal lineages were homologous. Accordingly, the contemporary germ cells are not PGCs but SGCs (secondary germ cells). While the following is speculative, I suggest that the original and truly primordial source of the germ cells was the gonad itself, an organ which is no longer competent as a germinal source.

I now turn to another aspect of reproduction which correlates favorably with the nonhomologous nature of the reproductive cells, namely, the cytogenetic mechanisms of sex determination.

### **The Independent Evolution of Sexual Reproduction**

Implicit in Darwin's theory is the assumption that sexual reproduction is the mechanism producing the differences that natural selection acts upon to produce the ultimately large differences we see in the living world. Attractive as the idea is, it has yet to be demonstrated that any creature reproducing by obligatory sexual means is capable of evolution beyond the generic level. I am well aware of the counter-arguments to this position which depend on there having been an insufficient period of time in which to observe such differences, a requirement which in effect renders the Darwinian hypothesis untestable. Accordingly, I am going to assume that sexual reproduction is incompatible with macroevolution simply in order to see where that premise leads with respect to what I have already presented.

First, there is no universal mechanism of sex determination. The birds and mammals have evolved opposite mechanisms of sex determination. In mammals the female is homogametic (XX), the male heterogametic (XY). In the birds it is the female which is heterogametic (ZW), the male homogametic (ZZ). These mechanisms involve heteromorphic sex chromosomes with the X and Z chromosomes being larger than their Y and W counterparts. Among the amphibia heteromorphic sex chromosomes are unknown but the cytogenetic mechanisms can be inferred from experiments involving sex-reversed animals. In the Anura, with the exception of *Xenopus*, which has a heterogametic female and a homogametic male, all have proved

to be of the mammalian type with a heterogametic male. All urodeles have proved to be of the bird type with heterogametic females. The experimentally produced WW class is female both in urodeles and in *Xenopus* (Ohno, 1967). In reptiles both male and female heterogamety have been described in lizards. In the Chelonia male heterogamety has been described in a few species. In other turtles in which heteromorphic sex chromosomes are unknown, sex is determined by the temperature during sensitive stages of incubation. In the primitive snakes heteromorphic chromosomes are unknown, while in the advanced snakes like the rattlesnake a ZW system operates as in birds. The literature on sex determination in vertebrates has been reviewed by Mittwoch (1983), and that review should be consulted for details. The point here is the correlation one can draw between the different modes of sex determination and the different sites of origin of the definitive germ cells in the same vertebrate taxa. I am not the first to call attention to the nonhomology of sex-determining mechanisms. Vorontsov (1973, p. 646), in the last paragraph of his review of the evolution of the sex chromosomes offers the following comments:

"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 is unclear whether the male species of different groups are homologous to each other or not; *they appear to be nonhomologous.*" (Italics are mine.)

### Semi-meiosis as a Mechanism for Macroevolution

Any theory of evolution must, it seems to me, accommodate in its postulates the nonhomologies I have discussed. I see no reason to question the evidence indicating the separate and independent evolution of sexual reproduction. The question then becomes, is there an asexual, or more precisely, a pre-sexual mode of reproduction which can serve to produce evolutionary change?

In 1940 Richard Goldschmidt published *The Material Basis of Evolution*. In it he charged that the neo-Darwinian mechanism has failed to explain the facts of evolution. Having been involved in the discovery of position effects on gene expression, he proposed that evolutionary change may be largely the result of genic rearrangement rather than point mutations in the genes themselves. According to Goldschmidt, such gene rearrangements

might result in what he called a "hopeful monster", a new and different creature produced in one or a few steps. While his views were not taken seriously by many in his lifetime, karyological studies support what he proposed. A recent study on the comparative structure of the chromosomes of the orang utan, gorilla, chimpanzee, and man has shown that the linear sequence of the euchromatic genetic material may be homologized to a very large extent in these animals (Yunis & Prakash, 1982). What is different between them is the relative position of blocks of genetic information. Most of the differences in the genetic structures have resulted from translocations and inversions of large and relatively few homologous regions of the chromosomes, a finding which vindicates Goldschmidt's views.

The question becomes, what sort of asexual mechanism can produce new gene arrangements in pairs in one or a few steps? I propose that the mechanism is provided by the first meiotic division or, in other words, by a semi-meiotic process. While the word meiosis has come to be virtually synonymous with sex since sexual forms employ meiosis for the production of gametes, in its original or primitive form the process may have had nothing to do with sex, but rather constituted an elegant device for the mandatory production of gene rearrangements as homozygotes in a single step. This potential is ensured by the fact that the sister strands or dyads always remain together in the first meiotic division. Consider, for example, the event of a chromosome rearrangement occurring in one of the chromosomes of an oogonial cell. Assuming the altered chromosome can partially pair with its unaltered homologue, it will be introduced as a pair into one half of the semi-meiotic products of that oogonial lineage, with the remaining products keeping the original chromosome constitution. The same can be said for duplications, deficiencies, translocations and of course point mutations. In short, any genetic alteration will be produced in the form of paired homologues in one half of the semi-meiotic products. Such a semi-meiotic lineage could go on indefinitely producing diploid paired rearrangements with the only restraint being the viability of the products. Figure 1 illustrates the formation of a new karyotype following a pericentric inversion in one chromosome of an oogonial cell. The semi-meiotic model also provides a means for the production of polyploids through the suppression of both meiotic divisions. Ohno (1967) presents convincing evidence that much of vertebrate macroevolution has involved either polyploidization or some other form of gene duplication, and he devotes a section of his book to the incompatibility between polyploidy and chromosomal sex-determining mechanisms. These difficulties are circumvented by the semi-meiotic model, as is the neo-Darwinian perspective that evolution is most likely to occur in small inbreeding populations.

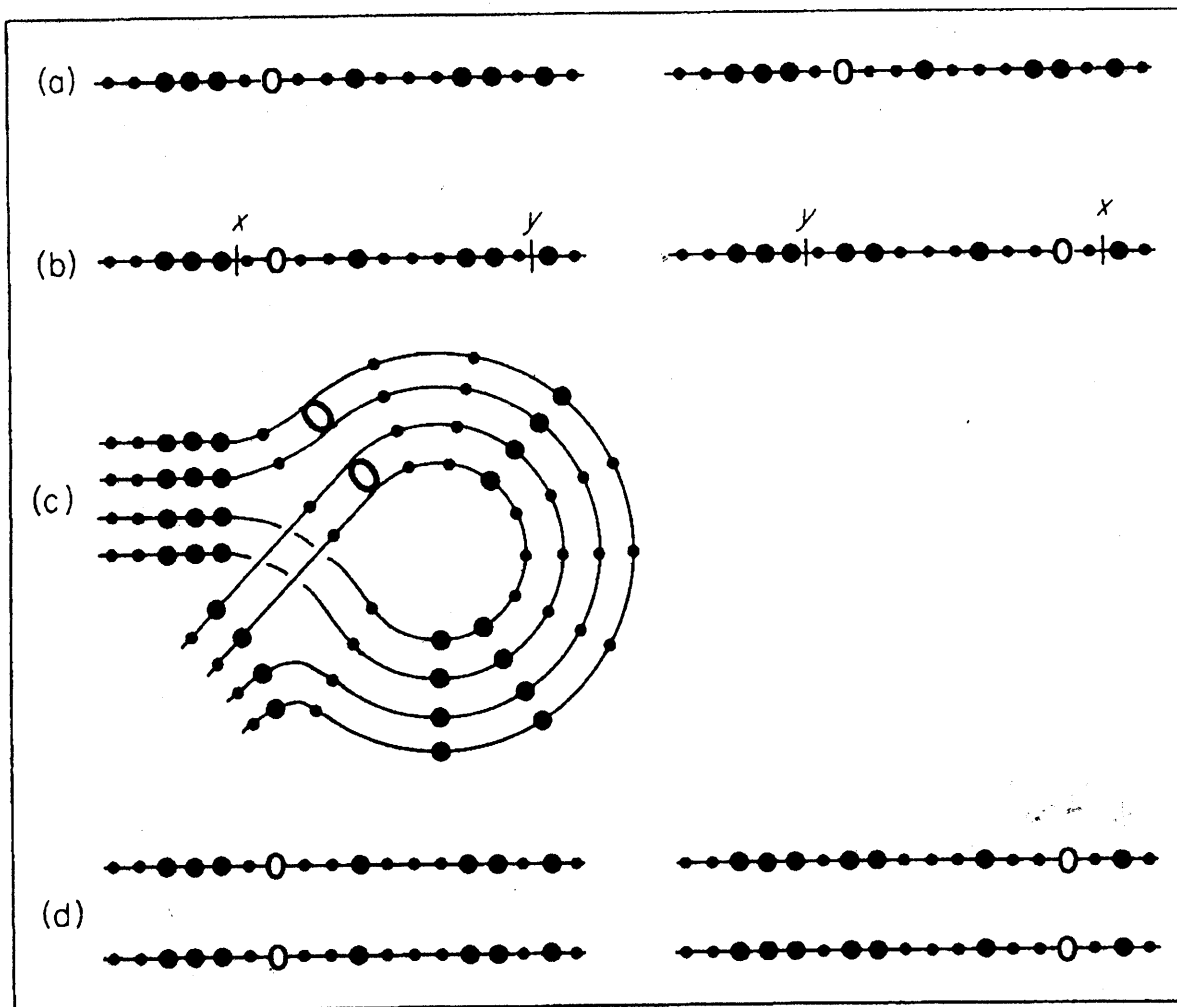


FIG. 1. The semi-meiotic formation of a new karyotype following a pericentric inversion in one chromosome of an oogonial cell. (a) Original karyotype. (b) Inversion heterozygote. (c) Tetrad configuration. (d) Products following the first meiotic division and duplication of the centromere. Left, original karyotype. Right, new karyotype.

The translocation or inversion of a chromosome segment is an all-or-none event, an occurrence which is incompatible with the Darwinian notion of gradualism. The semi-meiotic mechanism, moreover, remains compatible with the apparent absence of intermediate forms in the fossil record, and in fact suggests that such intermediate forms may not have existed, a view shared both by Goldschmidt (1940), and the paleontologist Schindewolf (1936).

#### The Evidence for the Semi-meiotic Mechanism

I will present two kinds of evidence for the semi-meiotic mechanism, the first indirect, the second direct. The indirect evidence rests on the observation that while the male gamete is invariably haploid in its functional state, the

female gamete is typically arrested at some stage prior to the completion of the second meiotic division and is reactivated to complete meiosis by the stimulus provided by the penetration of the sperm. In the amphibia as in humans the arrested state is in metaphase of the second meiotic division (Witschi, 1956). I suggest that the arrested state in oogenesis represents an evolutionary vestige from a time when either the sperm was not employed for activation or was employed solely for the purpose of activation but without the necessary contribution of genetic information.

The arrested state of the amphibian egg permits the experimental production of gynogenetic semi-meiotic progeny by activation of the egg with heavily irradiated sperm followed by the induced suppression of the second meiotic division (Nace *et al.*, 1970). These gynogens from a common mother are all genetically different from one another due not only to the random segregation of dyads during the first meiotic division but also due to crossing over which has preceded the first meiotic division. Amphibian material is ideally suited for a test of the semi-meiotic hypothesis, the only requirement being the production of heterozygous chromosome rearrangements in female frogs.

For the direct evidence I will select only two examples, one from the protozoa, the other from one of the most highly evolved of the vertebrates, the birds.

In 1947 L. R. Cleveland published a paper entitled *The Origin and Evolution of Meiosis*, a paper which has rarely been referenced since. His material was the flagellates which inhabit the gut of wood-eating insects. Of particular interest here are his observations on flagellates in the genus *Spirotrichosoma*, in particular those which occur in the gut of those termites of the genus *Stolotermes* found in New Zealand. Some of these flagellates are haploids, others are polyploids of the basic haploid number of 12. I quote Cleveland (p. 287):

"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. Why isn't this followed by a second meiotic division, thus returning the chromosomes to the haploid condition? The answer is simple: the centrioles are not duplicated until the chromosomes have also been duplicated and therefore reduction in chromosome number is impossible."

It is reasonable to assume that the polyploids were produced from the haploid forms by chromosome duplication. Since the polyploid forms reproduce semi-meiotically, these observations suggest the possibility,



remote as it may seem, that semi-meiosis may be a more primitive reproductive mechanism than diploid mitosis, a suggestion which remains compatible with the failure to observe evolutionary change in any diploid organism reproducing by mitotic means. In any event, the polyploid New Zealand species of *Spirotrichosoma*, since they reproduce strictly by semi-meiosis and have no sexual phase, constitute an important model for the mechanism I propose.

The second example is provided by the Beltsville strain of small white turkey which produces a very low percentage of parthenogenetic offspring, all of which have proved to be males (Olsen, 1965). Since in birds it is the female which is heterogametic (ZW) the mandatory production of males is clear in view of what is apparently a semi-meiotic process. If the ZZ dyad passes into the polar body the WW dyad remains in the egg. WW is presumably lethal in birds. If the WW dyad passes into the polar body leaving ZZ in the egg, activated eggs will of course develop into males. The evidence that the mechanism is semi-meiotic is provided by experiments by Olsen (1966), employing hens heterozygous for bronze plumage. The gynogenetic male progeny of these hens are of three types, white homozygotes, bronze homozygotes and bronze heterozygotes, with the latter class the result of a cross-over occurring prior to the first meiotic division. The mechanism is apparently identical to that in frogs except that in the turkey it is spontaneous. The turkey model also demonstrates the production of a chromosome homozygote (ZZ) from a heterozygote (ZW) in a single step.

### A Hypothetical Scenario for Evolution

Meiosis, like any other process involving more than one step, must have evolved in stages. I proceed with the reasonable assumption that the first meiotic division evolved before the second, and accordingly is the more primitive. Adhering to the semi-meiotic model, I suggest that major evolutionary changes occurred this way. With the invention of the second meiotic division sexual reproduction became mandatory and major evolutionary change came to a standstill. I propose further that the Weismanian germplasm is represented by the semi-meiotic lineage, one which may have had its origins in the gonad itself and that this cell lineage has been independently replaced by secondary and sexual lineages of extragonadal origin. Apparently in the course of evolution the competition between the semi-meiotic mechanism and the familiar complete meiotic mechanism has been won by the latter, perhaps due simply to the fact that the sexual mechanism permits outbreeding with its resulting heterosis. Thus the evolution of obligatory sexual reproduction becomes the self-limiting step in

the evolutionary process, leading to the curious conclusion that obligatory sexual forms have outcompeted the very life forms that made their existence possible. This hypothetical reconstruction raises an interesting question. Could there have been a time when these two cell lineages coexisted in the body? Such creatures could not only produce trial balloons but also fine tune them through the recombination of genes for which sexual reproduction is so admirably adapted.

Near the end of his career, Alexander Petrunkevitch (1952, p. 122) published a paper dealing with macroevolution and the fossil record of arthropods. His concluding comments are especially appropriate to the thesis developed here.

“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 distance 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 change.”

The semi-meiotic hypothesis constitutes a method which is indeed different from that employed for microevolutionary change. Furthermore, the hypothesis recognizes and incorporates into its structure the otherwise baffling evidence from comparative embryology and cytogenetics. Most important, unlike the neo-Darwinian hypothesis the semi-meiotic hypothesis is testable. In the last analysis all hypotheses must be either confirmed or disproved in the laboratory.

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#### REFERENCES

- CLEVELAND, L. R. (1947). *Science* **105**, 287.  
 DARWIN, C. (1871). *The Descent of Man and Selection in Relation to Sex*. New York: Appleton.  
 GOLDSCHMIDT, R. (1940). *The Material Basis of Evolution*. New Haven: Yale University Press.  
 LYELL, C. (1868). *Elements of Geology*. 6th Edn. New York: Appleton.  
 MITTWOCH, U. (1983). *Amer. Nat.* **122**, 159.  
 NACE, G. N., RICHARDS, C. M. & ASHER, J. H. JR. (1970). *Genetics* **66**, 349.  
 NIEUWKOOP, P. D. & SUTASURYA, L. A. (1979). *Primordial Germ Cells in the Chordates*. Cambridge: Cambridge University Press.  
 NIEUWKOOP, P. D. & SUTASURYA, L. A. (1981). *Primordial Germ Cells in the Invertebrates*. Cambridge: Cambridge University Press.

- OHNO, S. (1967). *Sex Chromosomes and Sex-Linked Genes*. Berlin: Springer-Verlag.
- OLSEN, M. W. (1965). *Brit. Poult. Sci.* **6**, 1.
- OLSEN, M. W. (1966). *Nature (London)* **212**, 435.
- PETRUNKEVITCH, A. (1952). *Am. Sci.* **40**, 99.
- SCHINDEWOLF, O. H. (1936). *Palaeontologie, Entwicklungslehre und Genetik*. Berlin: Bornträger.
- VORONTSOV, N. N. (1973). In: *Cytotaxonomy and Vertebrate Evolution* (Chiarelli, A. & Capanna, E. eds.). New York: Academic Press.
- WEISMANN, A. (1889). *Essays Upon Heredity*. Oxford: Clarendon Press.
- WITSCHI, E. (1956). *Development of Vertebrates*. Philadelphia: Saunders.
- YUNIS, J. J. & PRAKASH, O. (1982). *Science* **215**, 1525.