

Tribune libre

**Speciation burst hypothesis : an explanation
for the variation in rates of phenotypic evolution ⁽¹⁾**

S.C. TSAKAS* and J.R. DAVID**

* *Department of Genetics, Agricultural College of Athens, Athens, Greece*

** *C.N.R.S., Laboratoire de Biologie et Génétique évolutives, F 91190 Gif-sur-Yvette*

Summary

Phenotypic characters show remarkable variability in evolutionary rates and at times periods of seemingly random rapid acceleration. The speciation burst hypothesis offers a supported explanation of the variability of rates as being primarily the result of the organisms exposure and sensitivity to ultraviolet light and/or cosmic rays. Any major disruption increasing the amount of exposure such as a geomagnetic reversal would also increase the evolutionary rate. An association was found between a period of frequent geomagnetic reversals and rapid speciation events observed simultaneously in 2 different categories of organisms, with different habitats, and pronounced difference in population sizes.

Key words : Environmental mutagenesis, phenotypic evolution, geomagnetic reversals.

Résumé

*L'hypothèse d'une spéciation par bouffées : une explication
de la variabilité de la vitesse de l'évolution phénotypique*

Les caractères phénotypiques montrent une remarquable variabilité dans leur vitesse d'évolution et une accélération rapide à certains moments. L'hypothèse d'une spéciation par bouffées interprète cette variabilité comme la conséquence d'une exposition des organismes aux rayonnements ultra-violet et aux rayons cosmiques. Toute perturbation majeure, comme par exemple un renversement du champ magnétique terrestre, susceptible d'accroître l'exposition, provoquerait une accélération du taux d'évolution. Une association entre une période de changements fréquents du champ magnétique et des phénomènes de spéciation rapide est décrite dans 2 groupes d'organismes qui diffèrent à la fois par leurs habitats et leurs effectifs.

Mots clés : Mutations dues à l'environnement, évolution phénotypique, renversements du champ géomagnétique.

(1) S.C. TSAKAS dedicates this work to Pr C.B. KRIMBAS in gratitude for 25 years of collaboration.

I. Introduction

Phenotypic characters show not only a remarkable variability in evolutionary rates ranging from very slow to very fast, but in some cases periods of stasis interspersed with shorter periods of accelerated evolution. Evolutionary hypotheses dealing with phenotypic characters are needed to explain this variability. Such a hypothesis is speciation burst (TSAKAS, 1984) and in this paper its explanations and potential for prediction will be presented.

The most important population genetics parameter for differentiation-diversification-speciation is proposed to be mutation. According to this any major disruption increasing exposure such as geomagnetic reversals would accelerate evolution by increasing the mutation rate. During a geomagnetic reversal which may last from 1,000-10,000 years the biological material of the earth is exposed to more intense cosmic radiation (HARRISON & PROSPERO, 1974) and/or ultraviolet light (REID *et al.*, 1976). As a consequence, mutations with none, small, or great phenotypic effect will appear in a relatively short period of time. Mutations with great phenotypic effect explain the absence of transitional forms (missing links). At the same time, due to the heavy genetic load and/or environmental changes, many species become extinct. Population size does not appear to play such an important role under these conditions (KIMURA & OHTA, 1971). The population size parameter which has been used as a primary factor in explaining accelerated evolution has been called into question by recent findings on marine fossils; however these findings are consistent with the speciation burst hypothesis. These mainly are: strong correlations suggesting that during the Phanerozoic period a similar pattern of evolution had occurred simultaneously on a global scale (SEPKOSKI *et al.*, 1981); rapid evolutionary events have been observed in large populations containing millions of members (WILLIAMSON, 1981); sexually and asexually reproducing taxa show a similar pattern of speciation (WILLIAMSON, 1981).

II. Observations and explanations

Figure 1 shows the concurrence of a period of frequent geomagnetic reversals and accelerated evolutionary events observed simultaneously in 2 different categories of organisms, vertebrate and invertebrate, with different habitats, and pronounced difference in population size. VRBA (1980) reports a remarkable burst of speciation in Alcelaphini (antelopes) (see figure 2 A) during the period of 1.5-3.0 Myr which coincides with WILLIAMSON's (1981) data showing a rapid speciation event in Cenozoic molluscs in the Turkana Basin (see figure 2 B). In addition, rapid extinction also appears to have occurred during this period, resulting in a reduction in species duration. The majority of the species becoming extinct were from the newly formed ones. This 1.5 Myr interval of time representing approximately 1/3 of the 4 Myr span compared contains the greatest number, 13 out of 19, of geomagnetic reversals and these occurred in two clusters (COX, 1969).

The speciation burst hypothesis maintains that any factor affecting the amount or intensity of exposure to ultraviolet light and/or cosmic rays would affect speciation on a continuous basis as well as during geomagnetic reversals or other

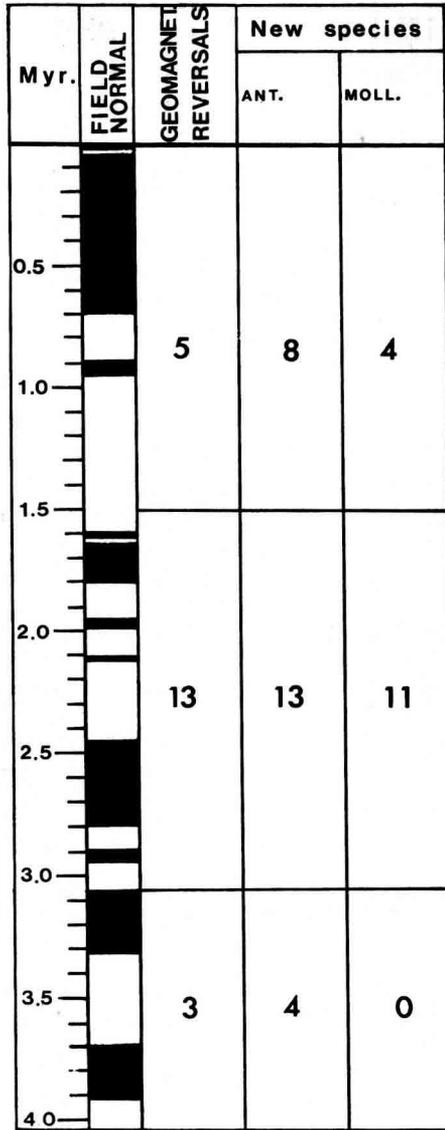


FIG. 1

The geomagnetic reversal pattern (COX, 1969) and the corresponding number of new species observed in antelopes (Alcelaphini) (VRBA, 1980) and molluscs (WILLIAMSON, 1981).

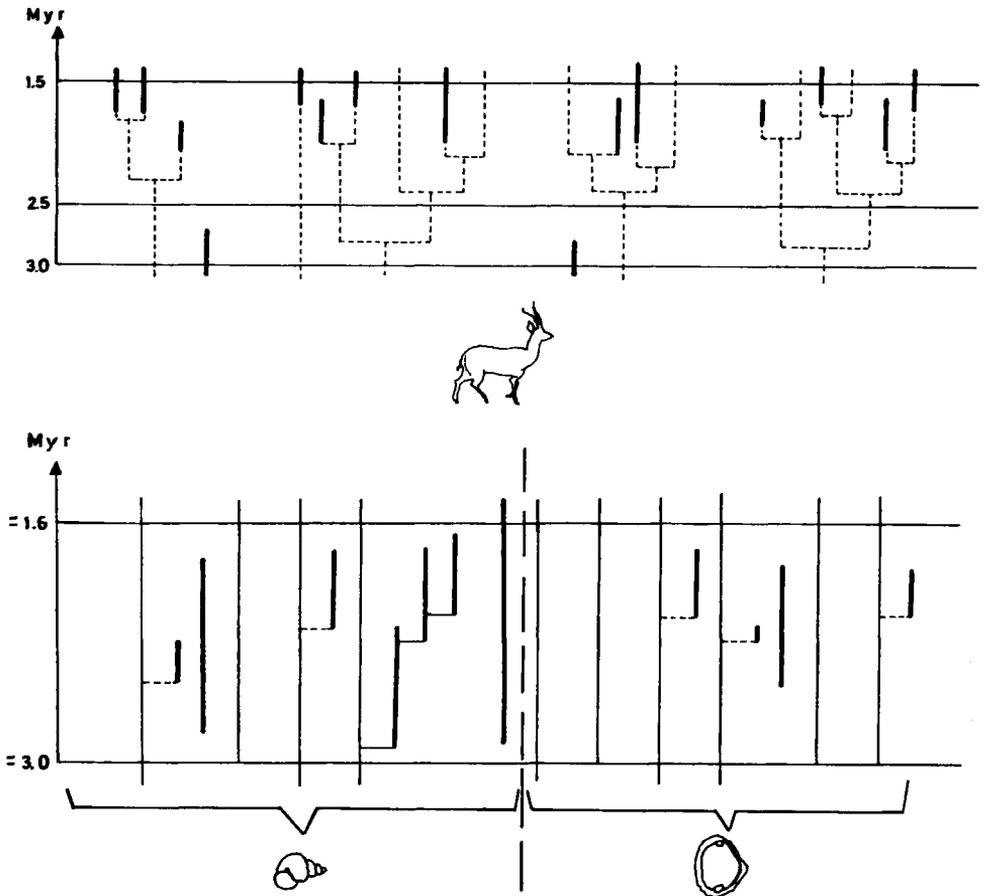


FIG. 2

Illustration of rapid speciation events during period of high geomagnetic reversals (1.5-3.0) (see fig. 1).

Solid lines represent species duration times.

Above : partial reproduction of VRBA's (1980) Alcelaphini group cladogram.

Below : partial reproduction of WILLIAMSON's (1981) patterns of evolutionary changes in Molluscs of the Turkana Basin.

major disruptions. The strong correlation observed between the rate of chromosomal evolution and rate of speciation in vertebrates (BUSH *et al.*, 1977) and in plants (LEVIN & WILSON, 1976) can be viewed from the following perspective. Ultraviolet rays produce mutations similar to the spontaneously arising ones, and ultraviolet light and cosmic rays are known to produce chromosomal aberrations. Chromosomal aberrations are a causal factor for speciation events (WHITE, 1980). This hypothesis then allows some preliminary predictions which are presented and followed by a brief account of supporting data.

A. Latitude

Speciation would be expected to be faster closer to the polar regions due to the morphology of the geomagnetic field which affords lower protection from cosmic rays in these regions in comparison to the equator.

HICKEY *et al.* (1983) found that new forms of animals and plants first appeared in the Arctic and migrated later to temperate climes. They report that data from the « Eureka Sound Formation in the Canadian high Arctic reveals profound difference between the time of appearance of fossil land plants and vertebrates in the Arctic and mid-northern latitudes. Latest Cretaceous plant fossils in the Arctic predate mid-latitude occurrences by as much as 18 million years, while typical Eocene vertebrate fossils appear some 2 to 4 million years early ».

In research dealing with 131 species of Benthic Foraminifera on the Atlantic Continental Margin of North America, BUZAS *et al.* (1984) found a shorter species duration and therefore faster evolutionary rate in the Northern regions spanning from Cape Hatteras to Newfoundland in comparison to that from Florida to Cape Hatteras. This appears to be continuous for the last 50 Myr period.

B. Depth of aquatic environment

Due to the protection afforded by water a progressively slower speciation-evolutionary rate would be expected moving from land to shallow water to deep water.

JABLONSKI *et al.* (1983) report that biological innovations occur nearshore and expand outward across the shelf in phanerozoic shelf communities. This can be described as an onshore speciation - offshore migration pattern.

Another aspect of the extensive research on benthic Foraminifera (BUZAS *et al.*, 1984) shows that evolutionary rates are greater in shallower than in deeper depths for the last 60 Myr. The combination of the 2 factors already described here, Northern latitude and shallow depth, showed the greatest evolutionary rates, observed as shortest species-duration time.

In figure 2, six of the seven newly-derived gastropods evolved from the species *Bellamyia unicolor*, *Cleopatra ferruginea*, and *Mellanoides tuberculata*. ABELL (1982) reports that these species have the following properties, a) they inhabit shallow water, b) they are capable of living over a wide range of pH and concentrations of dissolved salts, c) they are the most abundant of the Lake Turkana molluscs.

It is intriguing to note that whales as opposed to the landliving mammals studied by BUSH *et al.* (1977) show markedly reduced chromosomal and speciation rates which are found to be at the level of amphibia and reptilia.

C. Diurnal vs. nocturnal living habits

Due to the reduced exposure to ultraviolet light, it would be expected that nocturnal creatures would evolve at a slower rate than diurnal ones.

This could explain the significantly slower chromosomal and speciation rates observed in bats as compared with that of other land-living mammals; the rates were close to those estimated in amphibia and reptilia (BUSH *et al.*, 1977).

D. Sensitivity of the organism

It is predicted that the sensitivity of the organism to ultraviolet light and/or cosmic rays combined with the level of exposure would affect evolutionary speeds.

Studies show that in general mammals have the highest sensitivity to radiation (as measured by L.D.₅₀) and this declines through birds, reptilia and amphibia (CASARETT, 1968). Figure 3 shows the comparative diversification of the vertebrate subphyla mammalia, aves, reptilia and amphibia (VRBA, 1980) and this reflects their respective levels of sensitivity.

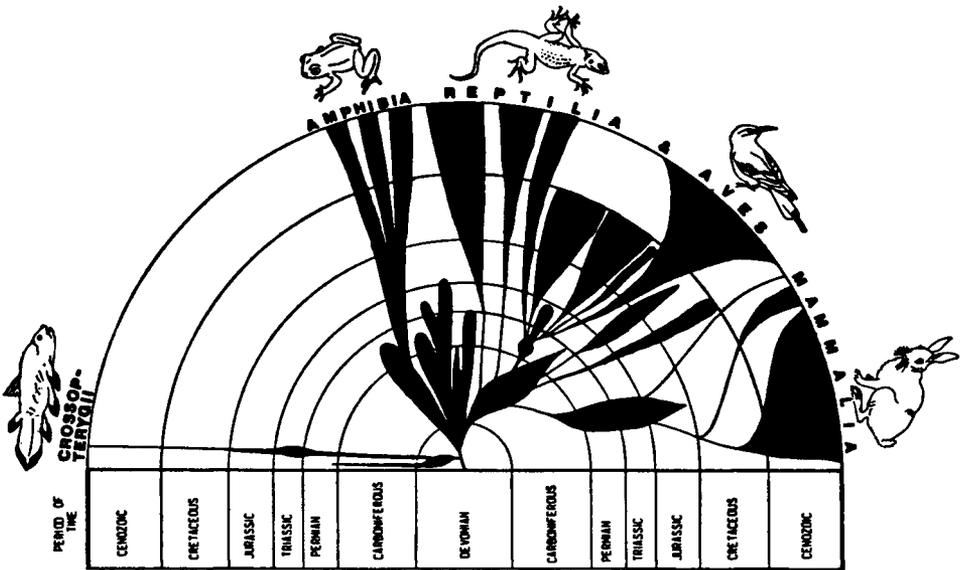


FIG. 3

The diversification of 4 vertebrate subphyla in comparison to the crossopterygian fishes (VRBA, 1980).

III. Conclusion

The speciation burst hypothesis offers a supported explanation for the remarkable variability in evolutionary rates seen in phenotypic characters as being a consequence of the exposure to and sensitivity of the organism to ultraviolet light and/or cosmic rays. The mitigating factors affecting exposure such as latitude, aquatic environment, living habits, and sensitivity of the organism give not only insight into the varying evolutionary rates but also offer preliminary guidelines for where and when forms of life would be expected to evolve at slower or faster rates. For example, the Crossopterygii (figure 3) whose exposure is mitigated by its more protected environ-

ment in the water and its scaled outer structure does not show any significant fluctuation in its evolutionary rate for the past 300 Myr but remains in stasis; and the same explanations may hold for another living fossil, the *Limulus polyphemus*, the horseshoe crab, which remains virtually unchanged for the past 230 Myr (VRBA, 1980).

The intriguing periods of acceleration in evolution can be seen as the result of increased exposure to ultraviolet light and/or cosmic rays due to some major disruption such as geomagnetic reversals. It has been demonstrated that pronounced acceleration in speciation in Alcelaphini and molluscs, which are 2 different categories of organism, with different habitats, and such a pronounced difference in population sizes, occurred simultaneously with a period of frequent geomagnetic reversals.

Received August 13, 1985.

Accepted March 20, 1986.

Acknowledgements

Frs. M. KIMURA, A. CAIN, D. WOODRUFF, and E. VRBA are thanked for their valuable comments and the reviewers for their useful remarks.

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