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18. W. Haymaker *et al.*, *Aerosp. Med.* **41**, 989 (1970).
 19. R. W. Young, *Sci. Amer.* **223**, 81 (October 1970); W. Haymaker, paper presented at the Ames Conference, Moffett Field, Calif., June 1970.
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Geomagnetic Reversals during the Phanerozoic

Abstract. *An analysis of worldwide paleomagnetic measurements suggests a periodicity of 350×10^6 years in the polarity of the geomagnetic field. During the Mesozoic it is predominantly normal, whereas during the Upper Paleozoic it is predominantly reversed. Although geomagnetic reversals occur at different rates throughout the Phanerozoic, there appears to be no clear correlation between biological evolutionary rates and reversal frequency.*

That the earth's magnetic field has reversed itself frequently in the past is now well documented (1). A geomagnetic polarity time scale has been established for the past 4.5×10^6 years by measuring the ages and magnetic polarities of volcanic rocks from many parts of the world (2). This time scale indicates that polarity changes occurred at a rate of about 5 per 10^6 years during the Late Tertiary. The application of the sea-floor spreading hypothesis (3) to marine magnetic anomalies on the basis of the Vine-Matthews crustal model (4) has led to the establishment of a geomagnetic polarity time scale for the whole of the Cenozoic (5). This time scale indicates that frequent reversals occurred during the Tertiary at a rate of about 3 per 10^6 years back to about 40×10^6 years ago, reducing to 1 per 10^6 years during the Early Tertiary. On the other hand, the Late Carboniferous and most of the Permian cover a period of about 50×10^6 years, a period dur-

ing which virtually no reversals occurred and which has been termed the Kiaman magnetic interval (6). The reality of this long reversed epoch has been confirmed by extensive measurements in the United States and Russia (7). The Cretaceous has also been identified as a period during which reversals occurred only very occasionally (8). In this report I present an analysis of all the paleomagnetic polarity measurements for the Phanerozoic in an attempt to establish some overall pattern in the behavior of the geomagnetic field.

Data for each geological period have been compiled from the tables of paleomagnetic results of Irving (9), which include all results up to 1963, and from subsequent lists produced by McElhinny (10) which include all results from 1964 to 1969. Added to these are 22 polarity results from the Cretaceous of the United States listed by Helsley and Steiner (8). In addition, results have been included from the synoptic tables

of the Russian paleomagnetic data (11), although it is difficult to decide in some cases which of these results have also been included in the other tables. There is the possibility that a small amount of duplication has occurred, but this will be unlikely to affect the conclusions drawn. In the analysis each entry in the tables of results was assigned unit weight, except that those entries which are a combination of others were excluded, as were those for which the magnetization either is known to have been acquired at a later date or is thought by the authors not to relate to the time of formation of the rock. This analysis of 1094 paleomagnetic results for the Phanerozoic is summarized by geological periods in Table 1. Where the precise ages of some igneous rocks are best known from isotopic dates, I have assigned these ages to the various geological periods, using the time scale of the Geological Society of London (12).

Each paleomagnetic result may be classified either as having normal polarity (N) where the magnetization is in the same sense as the present geomagnetic field, or as having reversed polarity (R) when the magnetization is in the opposite sense. In many instances both polarities occur in the one rock unit under investigation, in which case the result is listed as mixed (M). It is unlikely that paleomagnetic investigations will represent observations of the polarity over equal lengths of time. The investigations will represent the polarity over a range of intervals, and it might reasonably be assumed that this range of intervals will be approximately similar from one geologic period to the next. The observation of mixed polarities then gives some indication of the frequency with which reversals took

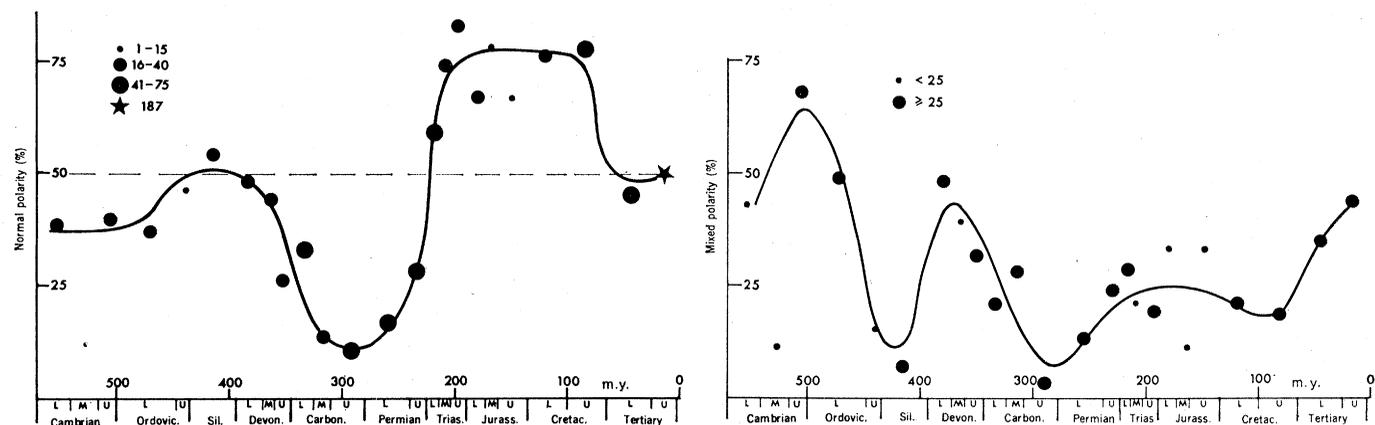


Fig. 1 (left). Percentage of normal polarity observed in worldwide paleomagnetic investigations for the Phanerozoic. The different symbols refer to the number of observations. Fig. 2 (right). Percentage of mixed polarity observed in worldwide paleomagnetic investigations for the Phanerozoic. The different symbols refer to the total number of observations.

place. The lists of Irving (9) and McElhinny (10) give the proportions of normal and reversed polarity measurements where both occur, so that it is possible to apportion the appropriate fraction of each mixed result to the figures for the normal and reversed polarities. Where this information is not available as with the Russian data (11), it is assumed that there is 50 percent of each polarity. For each geologic period the sums of the fractions of mixed measurements have been added to the respective normal and reversed occurrences and then rounded to the nearest whole number. The last two columns on the right-hand side of Table 1 indicate

the percentage of normal and reversed polarity measurements observed in each period and are a measure of the proportion of the time the geomagnetic field had that particular polarity.

The results of this analysis are illustrated in Fig. 1. For the Upper Tertiary (Miocene and Pliocene), 50 percent of the measurements have each polarity whereas in the Lower Tertiary 45 percent have normal polarity. For the mid-Carboniferous to Lower Permian, only a few measurements indicate normal polarity, the predominance of reversed measurements being related to the Kiaman magnetic interval (6, 7). Apart from the Lower Triassic, where fre-

quent reversals have been observed in the Moenkopi and Chugwater formations (13), the Mesozoic has predominantly normal polarity with 75 percent of the results in this category. Of particular interest is the Upper Triassic with 83 percent of the results showing normal polarity. This predominantly normal period probably contains a single reversed epoch which occurred close to the Triassic-Jurassic boundary, and which represents a horizon that could be of use in geological correlation (14). There is a marked difference between the Lower and Middle Devonian, which have roughly equal occurrences of normal and reversed polarity, and the Upper Devonian which has largely reversed polarity and marks the beginning of the predominantly reversed era until the close of the Paleozoic.

The results shown in Fig. 1 suggest a periodicity of about 350×10^6 years in the geomagnetic field during the Phanerozoic. The variation is remarkably regular and may have some fundamental significance. Crain *et al.* (15) have attempted a Fourier spectral analysis of a similar compilation of paleomagnetic polarity measurements undertaken some years ago by Simpson (16). However, Simpson took no account of the mixed measurements so that the number of results he was able to deal with was rather few. The spectral analysis indicated a sharp peak at 300×10^6 years, with a smaller peak at 75×10^6 years. Subsequently Crain and Crain (17) have created a new stochastic model for geomagnetic reversals based upon periods of 300×10^6 and 75×10^6 years; on the basis of their model they made a number of predictions regarding the Phanerozoic geomagnetic field. These predictions are not in general supported by the data presented here.

In Fig. 2 the percentage of mixed measurements is plotted as a function of time. The variation gives an indication of the frequency of reversals, and the pattern produced is not as simple as in the previous case; only one-quarter to one-third of the data can be used in this case. Several general conclusions can be drawn. Reversals were infrequent during the Upper Carboniferous and Permian, that is, during the Kiaman magnetic interval, as is already well known (6, 7). Reversals were also infrequent during the Upper Ordovician and Silurian. Frequent reversals seem to have taken place during the Upper Cambrian and Lower Ordovician, the Lower and Middle Devonian, and the Upper

Table 1. Polarity observed in 1094 paleomagnetic investigations for the Phanerozoic. The division of the occurrences of mixed polarity between the normal and reversed is indicated by the numbers with the plus sign in parentheses. N, normal; R, reversed; M, mixed.

Geological period	Number of occurrences			Overall percentage	
	N	R	M	N	R
<i>Tertiary (266)</i>					
Upper (187)	52(+41)	53(+41)	82(44%)	50	50
Lower (60)	16(+11)	23(+10)	21(35%)	45	55
Unspec. (19)	10(+2)	4(+3)	5		
<i>Cretaceous (102)</i>					
Upper (50)	35(+4)	6(+5)	9(18%)	78	22
Lower (38)	25(+4)	5(+4)	8(21%)	76	24
Unspec. (14)	12	2	0		
<i>Jurassic (58)</i>					
Upper (12)	5(+3)	3(+1)	4(33%)	67	33
Middle (9)	7	1(+1)	1(11%)	78	22
Lower (21)	11(+3)	3(+4)	7(33%)	67	33
Unspec. (16)	11	4(+1)	1		
<i>Triassic (127)</i>					
Upper (36)	25(+5)	4(+2)	7(19%)	83	17
Middle (19)	12(+2)	3(+2)	4(21%)	74	26
Lower (59)	26(+9)	16(+8)	17(29%)	59	41
Unspec. (13)	8(+1)	3(+1)	2		
<i>Permian (137)</i>					
Upper (59)	11(+6)	35(+7)	13(24%)	29	71
Lower (46)	2(+3)	38(+3)	6(13%)	17	83
Unspec. (32)	1	31	0		
<i>Carboniferous (179)</i>					
Upper (62)	5(+1)	55(+1)	2(3%)	10	90
Middle (39)	0(+5)	28(+6)	11(28%)	13	87
Lower (75)	18(+7)	41(+9)	16(21%)	33	67
Unspec. (3)	1	2	0		
<i>Devonian (82)</i>					
Upper (27)	1(+6)	14(+6)	12(32%)	26	74
Middle (18)	4(+4)	7(+3)	7(39%)	44	56
Lower (25)	4(+7)	9(+5)	12(48%)	48	52
Unspec. (12)	1	10(+1)	1		
<i>Silurian (28)</i>					
	14(+1)	12(+1)	2(7%)	54	46
<i>Ordovician (53)</i>					
Upper (13)	5(+1)	6(+1)	2(15%)	46	54
Lower (35)	3(+9)	15(+8)	17(49%)	37	63
Unspec. (5)	4	1	0		
<i>Cambrian (62)</i>					
Upper (25)	1(+9)	7(+8)	17(68%)	40	60
Middle (9)	0(+1)	8	1(11%)	12	88
Lower (21)	4(+4)	8(+5)	9(43%)	38	62
Unspec. (7)	3	3(+1)	1		
<i>Phanerozoic</i>					
Overall (1094)	337(+149)	460(+148)	337(30.8%)	44.4	55.6
Excluding Tertiary (828)	259(+95)	380(+94)	148(17.9%)	42.8	57.2

Tertiary, the last of which is especially well established (2, 5). It has been supposed that the sudden explosions and extinctions of species might be related to reversals of the geomagnetic field (16, 18), for during the polarity transition the shielding effect of the geomagnetic field is removed and the cosmic ray flux consequently is increased. The effect will obviously be enhanced when reversals occur frequently. A comparison of Fig. 2 with Simpson's (16) curves of the rate of organic evolution shows that there is no significant correlation with apparent reversal frequency. Accelerations in evolution seem to occur at times when the reversal rate has either maximum or minimum values.

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References and Notes

1. R. L. Wilson, *Geophys. J. Roy. Astron. Soc.* **7**, 194 (1962).
2. A. Cox, *Science* **163**, 237 (1969).
3. H. H. Hess, in *Petrologic Studies* (Geological Society of America, Boulder, Colo., 1962), pp. 599-620.
4. F. J. Vine and D. H. Matthews, *Nature* **199**, 947 (1963).
5. J. R. Heirtzler, G. O. Dickson, E. M. Herron, W. C. Pitman, X. Le Pichon, *J. Geophys. Res.* **73**, 2119 (1968).
6. E. Irving and L. G. Parry, *Geophys. J. Roy. Astron. Soc.* **7**, 395 (1963).
7. B. E. McMahon and D. W. Strangway, *Science* **155**, 1012 (1967); A. N. Khramov, *Izv. Akad. Nauk SSSR Fiz. Zemli* **1967**, 86 (1967); M. W. McElhinny, *Spec. Publ. Geol. Soc. Aust.* **2**, 61 (1969).
8. C. E. Helsley and M. B. Steiner, *Earth Planet. Sci. Lett.* **5**, 325 (1969).
9. E. Irving, *Paleomagnetism and Its Applications to Geological and Geophysical Problems* (Wiley, New York, 1964).
10. M. W. McElhinny, *Geophys. J. Roy. Astron. Soc.* **15**, 409 (1968); *ibid.* **16**, 207 (1968); *ibid.* **18**, 305 (1969); *ibid.* **20**, 417 (1970).
11. A. N. Khramov and L. Ye Sholpo, in *Paleomagnetism* (Nedra Press, Leningrad, 1967).
12. W. B. Harland, A. G. Smith, B. Wilcock, *Quart. J. Geol. Soc. London* **120s** (1964).
13. C. E. Helsley, *Geol. Soc. Amer. Bull.* **80**, 2431 (1969); M. D. Picard, *Amer. Ass. Petrol. Geol. Bull.* **48**, 269 (1964).
14. N. D. Opdyke and M. W. McElhinny, *Trans. Amer. Geophys. Union* **46**, 65 (1965); A. Brock, *J. Geophys. Res.* **73**, 1389 (1968).
15. I. K. Crain, P. L. Crain, M. G. Plaut, *Nature* **223**, 283 (1969).
16. J. F. Simpson, *Geol. Soc. Amer. Bull.* **77**, 197 (1966).
17. I. K. Crain and P. L. Crain, *Nature* **228**, 39 (1970).
18. R. J. Uffen, *ibid.* **198**, 143 (1963).
19. I thank F. E. M. Lilley for valuable discussions and comments on the manuscript.

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Regulation of Chromosome Replication in *Bacillus subtilis*: Marker Frequency Analysis after Amino Acid Starvation

Abstract. Marker frequency analysis of DNA isolated from amino acid-starved Bacillus subtilis cells shows that most chromosomes have not completed replication to the terminus. This finding agrees with earlier results concerning replication after amino acid starvation in this organism. The results are not compatible with regulation of chromosome replication at the initiation step only, and they suggest that a second regulatory circuit controls replication under conditions of amino acid starvation.

Chromosome replication, a controlled process which occurs during a definite interval of the cell cycle for higher organisms (1), is regulated during the sequence of growth and division in bacterial cells (2). The available information on the control of replication of the bacterial chromosome as well as other self-replicating units led Jacob and Brenner (3) to propose the *replicon model* to explain the regulated relationship between replication, cell growth, and cell division (4). A replicon is a unit of replication that may be equivalent to a bacterial chromosome. This model proposes a positive mode of regulation which involves, in its simplest form, a protein whose synthesis is directed by a structural gene on the replicon. This protein, called the initiator, interacts specifically with another region of the replicon, the

replicator, and triggers the beginning of the replication process. Once started, replication proceeds sequentially until the replicon has been duplicated. To begin another round of replication, a new initiator must trigger the replication before the process can start again.

If chromosome replication was regulated at the initiation step only, then blocking protein synthesis by amino acid starvation would stop new initiations but would allow replicons in the act of replication to continue until the replicon had been duplicated. Thus, a population of aligned replicons would

be produced that were completed and ready to be initiated again to start another round of replication. This approach has been used by many investigators to show that the chromosome of *Escherichia coli* is equivalent to a single replicon and that it has a unique, heritable site, the origin, from which replication is initiated (5). Some reports are incompatible with this conclusion, and they will be discussed later (6).

Yoshikawa and Sueoka (7, 8) have shown that the chromosome of *Bacillus subtilis* replicates from a unique origin in a sequential manner toward an identifiable terminus. My recent findings have led me to question whether control at the initiation step alone could account for the effect of amino acid starvation on chromosome replication in *B. subtilis* (9, 10). Chromosome replication following amino acid starvation was not synchronized from the known origin, as would be expected had they completed replication during the starvation period. This result prompted a closer examination of chromosome replication during amino acid starvation in *B. subtilis*. The marker frequency analysis developed by Sueoka and Yoshikawa is admirably suited to examine this situation (7, 11). If the initiation event serves as the only regulatory step in the control of chromosome replication, then blocking the initiator by blocking protein synthesis through starvation for a required amino acid would lead to a population of cells whose chromosomes are replicated to the terminus. The frequency of all genes would be the same, hence the ratio of any two genetic markers, as measured by marker frequency analysis, would be 1.0. Conversely, had chromosomes not completed their replication to the terminus, as is suggested by the earlier studies (9, 10), the ratio of a genetic marker located near the origin to another located near the terminus would exceed 1.0. Thus, marker frequency analysis provides an unambiguous choice between the two alternatives.

Table 1 lists the strains of *B. subtilis* used in this study. Conditions and media for growing cells have been

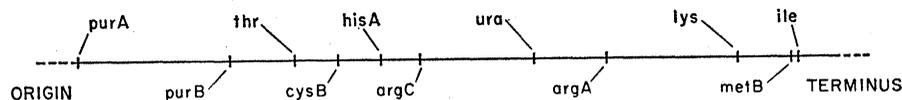


Fig. 1. Representation of genetic map for *B. subtilis* adapted from Dubnau *et al.* (13).