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The role of phyletic change in the evolution of *Pseudocubus vema* (Radiolaria)

David E. Kellogg

Abstract.—While the importance of allopatric speciation in the fossil record has long been underestimated, phyletic change within single unbranching lineages also occurs. The 50% increase in thoracic width observed in the radiolarian species *Pseudocubus vema* from an Antarctic deep-sea core is a clear example of a long-term phyletic trend in a continuous fossil sequence. Phyletic change in *P. vema* occurred at varying rates, but changes in the morphologic rate of evolution do not correspond to any obvious breaks in the fossil record such as would be indicated by missing segments of the core's magnetic stratigraphy. Variation in thoracic width, as measured by the coefficient of variation, does not depend on the morphologic rate of evolution, proportional rate of evolution, nor the amount of time required for the width to change by one standard deviation, so much as it depends on whether change was accomplished by addition or removal of extreme phenotypes to or from the population.

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Introduction

Phyletic change, defined as “change with respect to time of the characteristics of a species” (Bock, personal communication), is possibly the best documented aspect of evolution in the fossil record (Simpson 1953, p. 385). Examples of trends such as those observed by Simpson (1951) in Eocene to Recent Equidae are abundant in the paleontological literature. Yet despite its having been exhaustively described, the contribution of microevolutionary mechanisms at the infraspecific level to phyletic evolution has not been adequately analyzed. This omission is largely an artifact of the time scale on which phyletic trends have traditionally been observed. Only a small minority of the studies dealing with trends, such as those observed by Rowe (1899) in the echinoid *Micraster* from Late Cretaceous chalks of England or by Westoll (1950) in the Mesozoic oyster *Gryphaea*, are based on data from continuous deposits. Most, especially those studies of large land vertebrates of which only a relatively few specimens are found at a single outcrop, tend to incorporate samples from widely separated localities and times. In his well known study of the trend towards hypsodonty in North American Equidae,

Simpson (1951) drew comparisons between data from an early Eocene sample from Wyoming, a middle Oligocene sample from South Dakota, and both a late Miocene and a late-early or early-middle Pliocene sample from Nebraska, no two of which were assigned to the same genus. There were only fourteen specimens in the largest of these samples; the smallest contained four. The study clearly documents a long-term trend, but such large temporal and spacial discontinuities tend to filter out small-scale evolutionary changes occurring at or below the species level. Consequently although phyletic trends are the cumulative result of such microevolutionary mechanisms as directional selection, drift, or mutation pressure within single populations, most examples of phyletic change in the fossil record have only been observed, *ex post facto*, at the level of the genus or above.

More recently, Eldredge (1971) and Eldredge and Gould (1972) have proposed as an alternative to evolution by “phyletic gradualism,” a concept of “punctuated equilibria,” which they believe to be more in keeping with the discontinuous nature of the fossil record. I agree with Eldredge and Gould that there are

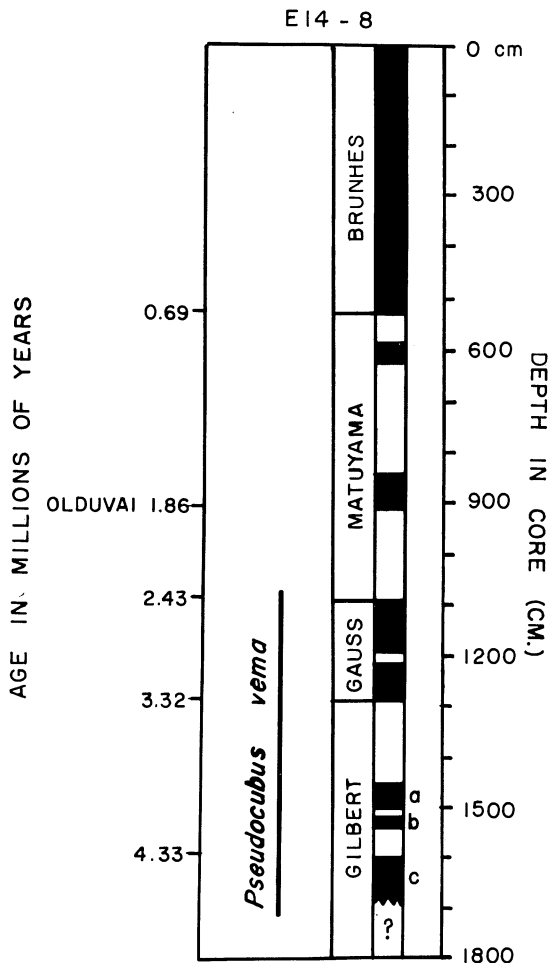


FIGURE 1. Magnetic stratigraphy of core E14-8 showing the stratigraphic range of *Pseudocubus vema* (after Hays and Opdyke 1967). Black indicates normal polarity; white, reversed polarity.

numerous gaps in the fossil record which may be attributed to allopatric speciation (Kellogg, in press). But I must also agree with Bock (personal communication) that it is fallacious reasoning to place allopatric speciation in direct opposition to phyletic change. As Bock pointed out, the two processes are simply not alternatives. Phyletic change does not in and of itself lead to the appearance of new species, but it is an integral part of both the allopatric and sympatric phases of speciation. More easily recognized is phyletic change occurring over long periods of time in lineages which are not undergoing speciation.

The purpose of this study is to demonstrate the origin of phyletic trends at the species level

by presenting and analyzing a trend within a single species of fossil Radiolaria from an Antarctic deep-sea core. Deep-sea cores provide excellent material for this type of study because they often contain continuous or nearly continuous records, millions of years long, of large populations of microfossils from a single locality together with an equally long magnetic record (Figure 1). This magnetic record makes it possible to accurately sample the continuous microfossil sequences in the cores at fine enough intervals of time to allow the observation of specific phenotypic changes which can be interpreted as the predictable results of the action of microevolutionary mechanisms within single populations.

Choice of Core and Oceanographic Setting

Core E14-8 was chosen for this study because it contained both a clear magnetic record and a nearly continuous Antarctic radiolarian sequence for roughly the past 4.5 million years. Of the long Antarctic cores available at the Lamont-Doherty Geological Observatory, E14-8 contains the most complete microfossil record (Hays and Opdyke 1967).

E14-8 was taken from the western flank of the East-Pacific Rise at 59°40'S, 160°17'W (Figure 2) in 3875 meters of water. The dominant influence on surface water circulation in this region is the Antarctic Circumpolar Current, which, driven by westerly winds, circles the Antarctic Continent between about 40° and 60°S latitude. The antarctic polar front is a zone of convergence which develops between the denser (cooler) Antarctic water and the less dense (warmer) subantarctic water (Neumann and Pierson (1966, p. 465)). This convergence is very stable. Hays (1965, p. 163) found no indications of any significant southward shift in the position of the Antarctic polar front during the last 4 to 5 million years. Furthermore, he found that this convergence forms an effective geographic barrier between Antarctic radiolarian species restricted to the cold water south of the convergence and the warm water species of the subantarctic region north of the convergence.

Surface water temperature appears to be the major factor in determining the distribution of radiolarian species north and south of the Antarctic polar front. Within the cold waters

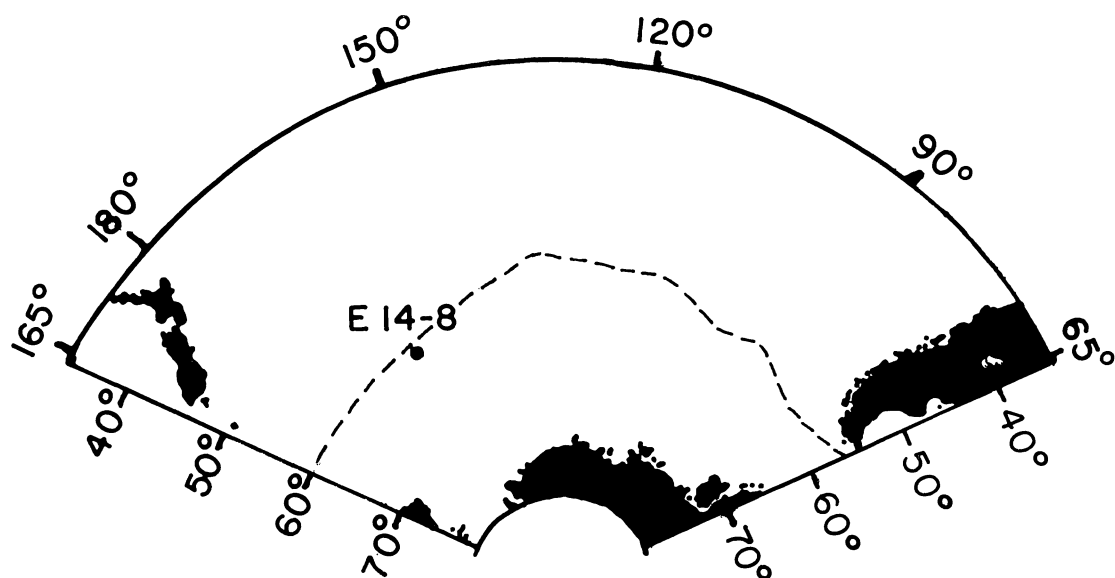


FIGURE 2. Location of core E14-8 with respect to the Antarctic convergence (after Hays and Opdyke 1967). Dotted line indicates position of the convergence.

south of the convergence, the Antarctic species discussed by Hays (1965) have circumpolar distributions and are not restricted to localized sectors of the Antarctic region. Hays and Opdyke (1967) found that extinctions and first appearances of stratigraphically important radiolarian species occurred at the same times relative to the magnetic time scale in each of three long cores from different latitudes in Antarctic waters.

At present, physical oceanographic parameters for the Antarctic surface waters are highly stable over short periods of time. According to Gordon et al. (1970), the temperature at a depth of 20 meters ranges between -1.5°C near the Antarctic Continent and 7 or 8°C at 50°S in the winter and between -1.5°C and 9 or 10°C at the same latitudes in the summer. The small difference between summer and winter temperatures is due largely to the melting of pack ice during the summer months; this tends to prevent any significant amount of warming of the surface waters. Similarly, the salinity of the surface waters ranges from a little less than 34.0‰ to 34.4‰ summer and winter, although the overall summer salinity is somewhat lower than the overall winter salinity because of seasonal addition of relatively fresh water from melting pack ice. Dissolved oxygen content remains between 8.0 ml/l and 6.5 ml/l all year

around. Furthermore, because cooled surface water is constantly sinking to the bottom to become Antarctic bottom water, no thermocline develops in Antarctic waters during the course of the year.

If conditions were equally stable in the past, one might reasonably assume that most evolutionary changes in Antarctic Radiolaria came about as adaptations to long-term shifts, such as warming or cooling trends of long duration, in an environment which did not show any significant change over the course of a single year. The presence at depth in an Antarctic core of radiolarian species which are presently restricted to the warmer waters north of the Antarctic polar front would be a good indication that warmer conditions prevailed in the Antarctic region in the past. Hays and Opdyke (1967) found "no strong evidence in E14-8 of warmer conditions at depth, but below 1100 cm (2.4 million years B.P.) several warm-water Radiolaria occur intermittently down to the point where the core becomes (almost) barren (of Radiolaria) at 1710 cm." Bandy et al. (1971) also found evidence of warm-water Radiolaria near the bottom of E14-8. The species with which this study is concerned became extinct in E14-8 shortly above 1100 cm.

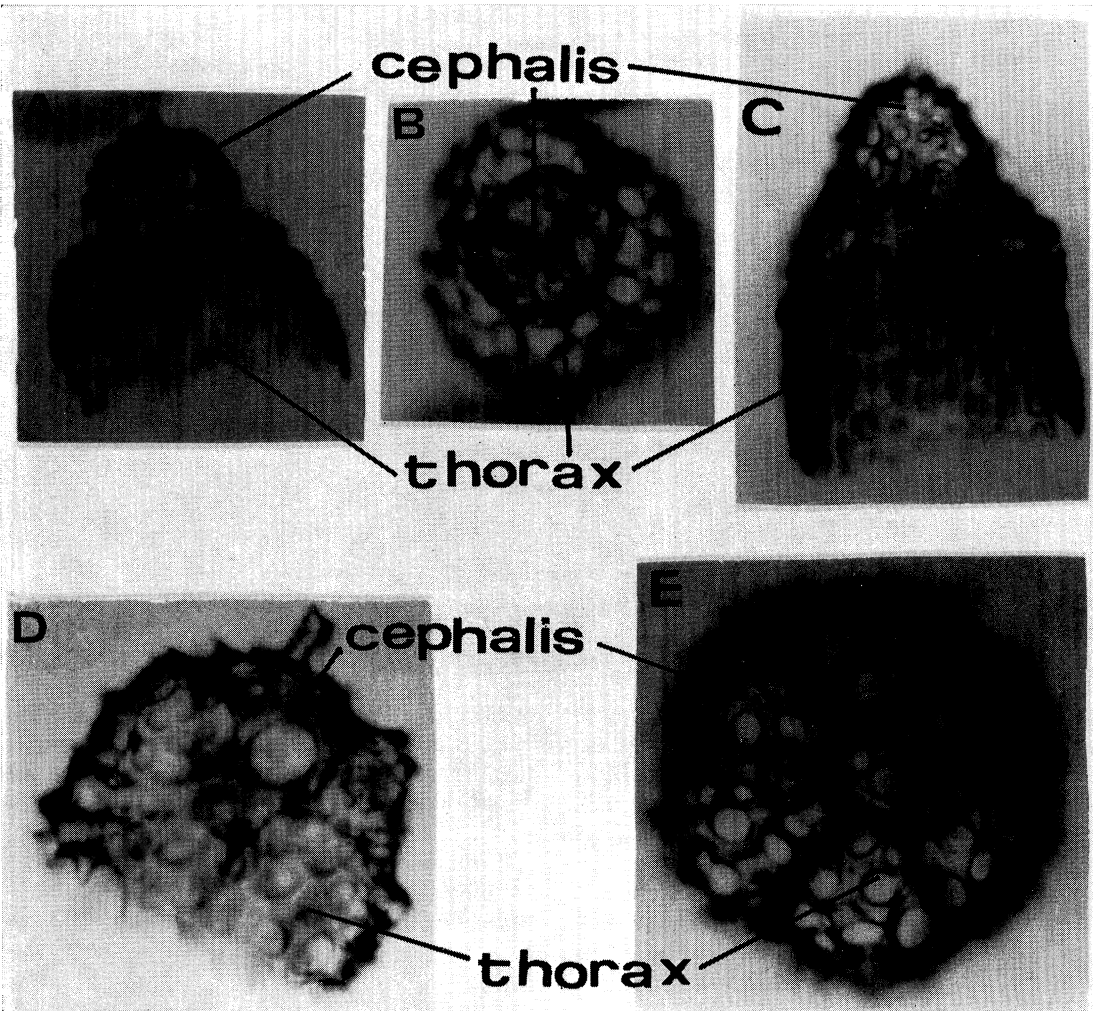


FIGURE 3. *Pseudocubus vema*. a. *P. vema* from E14-8, 1770 cm, side view. b. *P. vema* from E14-8, 1770 cm, top view. c. *P. vema* from E14-8, 1420 cm, side view. d. *P. vema* from E14-8, 1085 cm, side view. e. *P. vema* from E14-8, 1085 cm, top view.

Systematics

This study concerns the radiolarian species *Pseudocubus vema* (Hays 1965). The skeletal structure, taxonomic affinities, and stratigraphic and geographic ranges of *P. vema* have been described in numerous previous papers (Hays 1965; Opdyke and Hays 1967; Keany and Kennett 1972; Dumitrica 1973).

The choice of *P. vema* as the subject of this study was determined by the following three considerations:

1.) *P. vema* has a long stratigraphic range in Antarctic deep-sea cores; extending from at least the Gilbert "c" event, about 4.5 million years B.P., to the base of the Matuyama

reversed epoch some 2.4 million years B.P. (Figure 1). This range is the same in all three long Antarctic cores from different latitudes in the Antarctic studied by Hays and Opdyke (1967). *P. Vema* is now recognized as an important stratigraphic indicator species in Antarctic sediments.

2.) Throughout its entire stratigraphic range, *P. vema* was confined to the cold water south of the Antarctic polar front.

3.) The skeleton of *P. vema* underwent considerable change in shape between the first appearance of this species at the base of E14-8 at 1790 cm and its last appearance at 1085 cm (compare Figures 3a and 3e). At the beginning of its range *P. vema* had a skeleton which con-

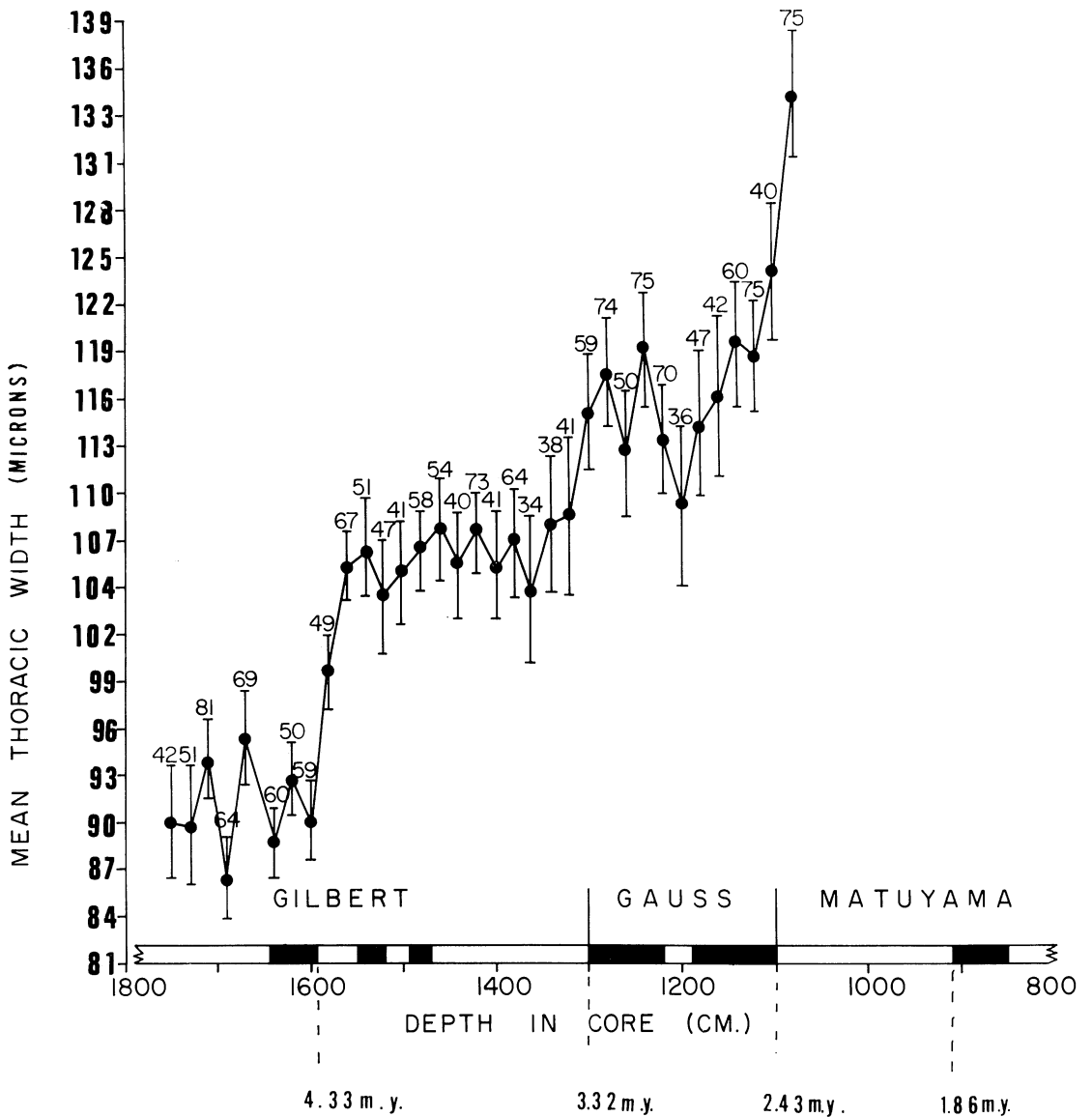


FIGURE 4. Mean thoracic width of *P. vema* vs. depth in core E14-8. Vertical lines through points indicate 95% confidence intervals for means. Numbers above lines indicate number of specimens in sample. Time line across bottom shows depth at which magnetic reversals occurred.

sisted of a prominent cephalis and narrow thorax (Figure 3a and b). By the time of its last appearance, the cephalis had receded into the thorax, and the thorax itself had undergone an increase of 50% in width.

Determination of the manner in which the change in thoracic width was accomplished, as well as the magnitude, direction, and rate of change are the major goals of investigation in the following sections of this study.

Methods

Sampling.—Samples of between one and two cm³ were taken at intervals of approximately 20 cm down E14-8. This interval seemed reasonable for initial sampling in light of the sedimentation rates in the core (Table 1). If on subsequent examination this sampling interval proved too coarse to reveal the details in which I was interested, additional

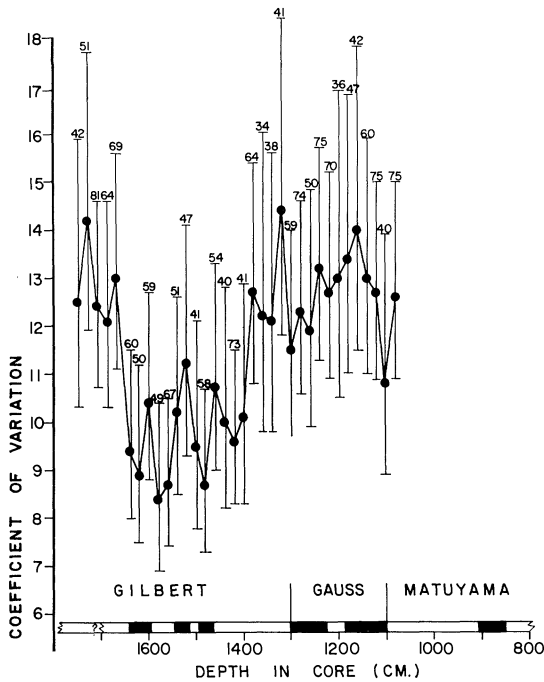


FIGURE 5. Coefficients of variation of thoracic width of *P. vema* vs. depth in core E14-8. Vertical lines through points indicate 90% confidence intervals for coefficients. Numbers above lines indicate number of specimens in sample.

samples could always be taken to reduce the interval to 10 or even 5 cm if necessary.

Each sample was boiled in about 200 ml of water to which 10 ml of sodium hexametaphosphate ("Calgon") had been added until the sediment became disaggregated. The disaggregated sediment was sieved through a 63 micron mesh and the residue agitated sonically and sieved once again. The remaining

coarse fraction was allowed to settle in about 20 ml of water. A few drops of the residue was placed on a glass slide, allowed to dry on a warm hotplate, and then covered with Canada balsam and a glass cover slip.

No sample within the geologic range of *P. vema* contained less than 35 specimens of this species except for the two oldest samples (1790 and 1770 cm) which were taken from the region of E14-8 below 1710 cm (a region Hays and Opdyke (1967) described as "barren"). Since there was only one specimen of *P. vema* in the sample from 1770 cm and none in the sample from 1790 cm, it seemed unlikely that even one or two additional samples from these levels could provide enough specimens to be worth analyzing statistically. Furthermore, as there was only a very little material left at these two levels, it did not seem practical to sample them twice. All slides examined for this study are in the possession of Dr. James Hays of the Lamont-Doherty Geological Observatory.

Statistical Analysis.—For each specimen of *Pseudocubus vema*, the width of the thorax at its widest point was measured with an eye-piece micrometer at a magnification of 400×. The mean width and the Pearsonian coefficient of variation were then calculated for each sample and plotted against depth in core (Figures 4 and 5 respectively). Since the number of specimens in each sample varied between 35 and 82, 95% confidence intervals were determined for the mean of each sample (Figure 4). The mean sample width was also plotted against time in millions of years in Figure 4, and the rate of size increase, proportional rate

TABLE 1. Ages of magnetic reversals in E14-8. Dates of magnetic reversals according to Opdyke (1972). Magnetic stratigraphy of core E14-8 from Hays and Opdyke (1967).

Reversal	Depth in E14-8 (cm)	Date (my)	Time interval (my)	Sedimentation rate (cm/yr)
Top Matuyama	535	.69	1.74	10/30,797
Top Gauss	1100	2.43	.89	10/44,500
Top Gilbert	1300	3.32	1.01	10/33,115
Top Gilbert "c"	1605	4.33		
Base Olduvai	915	1.86	2.47	10/35,797

TABLE 2. Rates of evolution of greater thoracic width by *Pseudocubus vema* in E14-8.

Depth in core (cm)	Interval between samples (cm)	Width thorax <i>P. vema</i> (microns)	Change width thorax (microns)	Time between samples (yrs)	Rate of change of width (microns)	Proportional rate of change (%/yr)	Standard deviation	Time to change one standard deviation (yrs)
1750	150	89.81	0.11	496,722	.22	.00247	11.19	4.52×10^6
1600	40	89.92	15.75	132,459	118.90	1.21849	9.33	7.52×10^6
1560	220	105.67	2.84	728,526	3.89	.03349	9.16	3.90×10^6
1340	60	108.28	9.13	221,459	41.22	.36553	13.05	3.94×10^7
1280	135	117.41	1.92	600,750	3.19	.02699	14.41	5.74×10^6
1145	60	119.33	15.34	246,445	62.24	.49069	15.51	3.46×10^7
1085		134.67					16.99	

of size increase, and amount of time required for a size increase of one standard deviation were calculated (Table 2). Lastly, a size frequency diagram was drawn for each sample (Figure 6). All calculations were converted from eyepiece micrometer units to microns. The conversion factor used was 100 eyepiece micrometer units = 290 microns at a magnification of 400×, so that a typical specimen of *P. vema* 40 units wide would measure approximately 116 microns across.

Dating.—As evolutionary rates were to be calculated, the dating of samples was of primary importance. The magnetic stratigraphy of E14-8 (Figure 1) was originally determined by Opdyke and Hays (1967). All of the known magnetic epochs and events of the last 4.5 million years are present in sequence in this core, from the Gilbert “c” event to the Brunhes normal epoch, with the single exception of the Kaena reversed event of the Gauss normal epoch (see Opdyke 1972 for a complete magnetic stratigraphy for the past 5 million years). While it is possible that the lack of evidence for the Kaena event in E14-8 is caused by a short hiatus within the Gauss, it often happens that a relatively short event like the Kaena (.085 million years long) is not detected in a core because the samples are too widely spaced or have too low a magnetic intensity to yield conclusive results.

P. vema ranges from 1790 cm near the base of E14-8 to 1085 cm, just above the base of

the Matuyama reversed epoch. On the basis of Opdyke’s (1972) dates of 4.33 million years B.P. for the top of the Gilbert “c” event which occurs at 1605 cm in E14-8 and 2.43 million years B.P. for the base of the Matuyama, this range would represent more than 2 million years. The full extent of the stratigraphic range of *P. vema* in E14-8 is not known because the magnetic intensity drops too low to give reliable results in samples from below 1640 cm, and the ages of samples from the older part of the core (Table 1) must be extrapolated from this point on the assumption that the sedimentation rate between 1750 and 1605 cm was roughly the same as that between 1605 and 1300 cm. The problem of dating the lower portion of E14-8 is further complicated by a possible hiatus at about 1700 cm (personal communication, Hays). Given these uncertainties, the lowest meter of core might be considerably older than my estimate (Figure 4), and my calculations of rates of evolution (Table 2) over this last meter would represent a maximum.

Aside from the possible absence of the Kaena event, time control for the upper 16½ meters of E14-8 is excellent. Between 1605 and 915 cm, which corresponds to the base of the Olduvai event at 1.86 million years B.P., the rate of sedimentation averages about 10 cm every 35,000 years. Accordingly, there would be an average interval of only 70,000 years between samples taken 20 cm apart from the

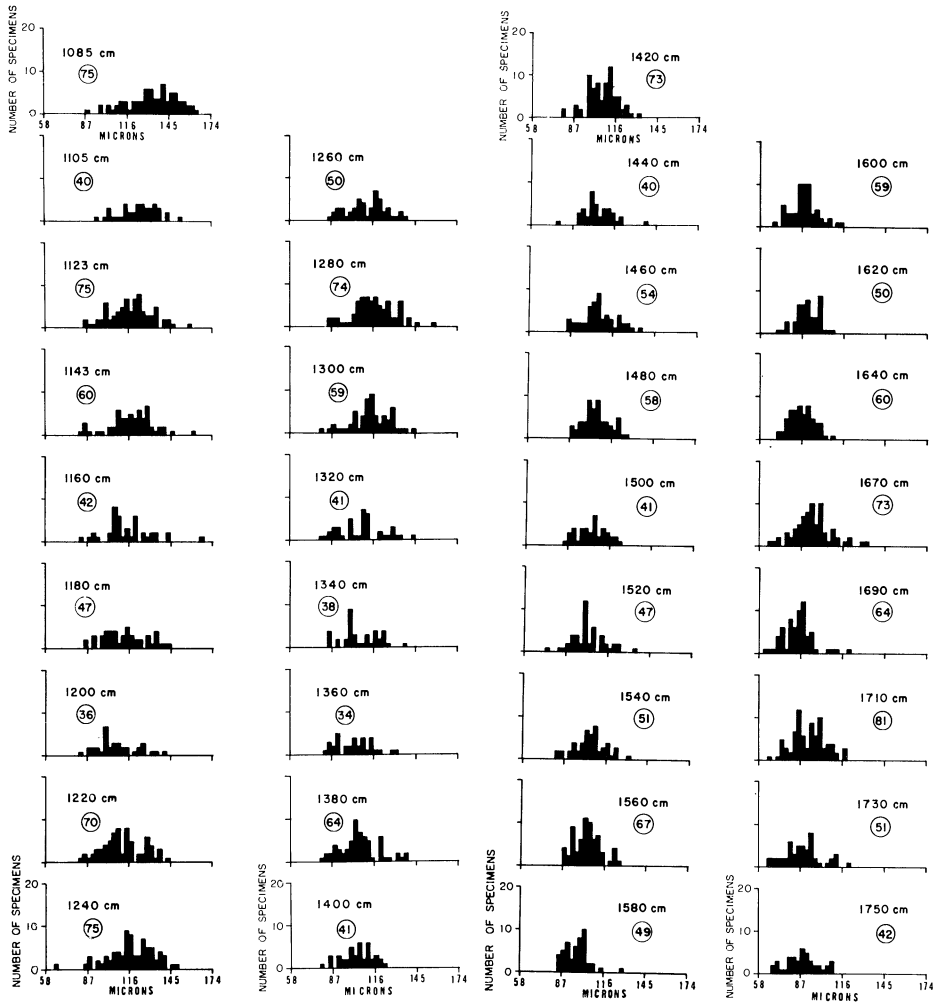


FIGURE 6. Frequency distributions of thoracic widths in samples of *P. vema* from core E14-8. Numbers in circles are sample sizes.

lower half of E14-8. The rate of sedimentation was, of course, not invariable over the entire range of *P. vema*. Table 1 lists the average sedimentation rates for the Matuyama, Gauss, and Gilbert epochs in E14-8 individually.

Results

The results of the calculations outlined above are presented in graphic form in Figures 4 through 6 and summarized in Table 2.

Rates of evolution.—In Figure 4 the mean thoracic width of *P. vema* is plotted against depth and time in core E14-8. The single feature which dominates both of these graphs is a strong trend toward increased size running the entire length of the stratigraphic range of *P. vema* within the core. In the course of this

trend, the thoracic width of *P. vema* increased from 89.81 microns at 1750 cm to 134.68 microns at 1085 cm, an increase of about 50% in something over two million years. The line connecting the point at 1750 with that of 1085 cm is not straight but “stepped” indicating that increased width was evolved by *P. vema* in fits and starts rather than at a steady rate. Specifically, most of the change occurred during three short bursts of rapid evolution at 1600–1560 cm, 1340–1280 cm, and 1145–1085 cm. These bursts were preceded and/or followed by extended periods three or four times as long as the bursts, during which the mean fluctuated between more or less narrow limits.

The rates of change during periods of rapid evolution (Table 2) were generally on the

order of 15 to 540 times faster than at other times. Similarly, the proportional rates of change as calculated by the formula:

$$R_{\text{prop}} = \frac{\log_e x_2 - \log_e x_1}{T} \quad (\text{Haldane 1949, p. 52}) \quad (1)$$

(where x_1, x_2 are the sample means at t_1, t_2 , respectively; T is the amount of time between t_2 and t_1 ; the R_{prop} is the proportional rate of change in a given measurable character over time T) were one to three orders of magnitude faster during the bursts of rapid change.

The amount of time required for the mean width of *P. vema* to increase by one standard deviation as calculated by Haldane's (1949, p. 58) formula:

$$T_{1 \text{ S.D.}} = \frac{VT}{\log_e x_2 - \log_e x_1} \quad (2)$$

(where T, x_1, x_2 have the same meaning as in the formula for proportional rate of change; V is the standard deviation of values for a given measurable character in a sample of the population at time t_1 ; and $T_1 \text{ S.D.}$ is the time it would take the sample mean for that character to change by amount V [one standard deviation] at the calculated proportional rate of change between t_1 and t_2) was one to three orders of magnitude longer in the intervals between the bursts than during them.

Variation.—A widely used estimate of the amount of variation for a given morphological feature in a population is the Pearsonian coefficient of variation:

$$C = 100 \times \frac{\text{sample standard deviation}}{\text{sample mean}} \quad (3)$$

(Simpson 1953, p. 68).

Between 1750 and 1085 cm, the coefficient of variation for thoracic width of *P. vema* increased by only .1293. But the shape of the curve for this parameter, concave between 1750 and 1400 cm and convex between 1400 and 1085 cm, suggests that the range of *P. vema* in E14-8 may be divided into a period of relatively low variation below 1400 cm and a period of greater variation above this point (Figure 5). The integral relationship between change in the mean thoracic width and the range of variation is graphically illustrated in Figure 6 and will be discussed at length in the following section.

Discussion

Bock (personal communication) defines phyletic evolution as follows: "Change with respect to time of the characteristics of a species is phyletic evolution; hence modification along the time axis of a single phyletic lineage is phyletic evolution." Furthermore, "Rates of phyletic evolution vary greatly at different times in different subdivisions of the same lineage. These rates may vary from no detectable phenotypical change for long periods to rapid modifications over short periods of time such as those achieved in animals and plants under domestication. But they exclude large, single-step changes from one morphological condition to another as suggested in theories of saltation." The 50% increase in the mean thoracic width of the radiolarian species *Pseudocubus vema* which occurred during the roughly two million years this species inhabited Antarctic waters fits this description of phyletic change very closely. Observed changes in rate of morphologic change probably do not indicate gaps in the fossil record since there are no corresponding gaps in the magnetic stratigraphy. Because the Radiolaria have relatively simple morphologies, they may appear to have evolved at slower rates than more complicated animals (Schopf et al. 1975). They were once thought to be "living fossils." Yet when studied on the proper time scale, it is clear that they have been evolving at perceptible and varying rates, as might be expected of any organism under the influence of natural selection.

Explanation of the shape of a population-level trend.—The trend towards increased width in *Pseudocubus vema* is "stepped" rather than straight, indicating a variable instead of a constant rate of evolution. Short periods of very rapid evolution alternated with longer intervals during which relatively little change occurred.

The variability of the rate and direction of evolution of *P. vema* is easily explained. At each point along these curves, both the rate and the direction of evolution were determined by the strength and direction of prevailing selection forces. The trend itself is merely the vector summation of the change at each point. Ideally, there should be a point for each generation. But, assuming *P. vema* had only one generation per year (which is a

conservative estimate for a protist—Casey et al. [1970] reported turnover rates of one month or less for Radiolaria in sediments of the Santa Barbara Basin), the amount of time required to measure and analyze over two million samples would be prohibitive even if sedimentation rates for the Antarctic were such that intervals of time as small as one year could be resolved. In any case, the three main conclusions drawn from the analysis would most likely remain unchanged:

1.) Strong evidence for long term phyletic change may be observed in lineages whose fossil records are relatively complete.

2.) A trend really only becomes a trend in retrospect. That is, each generation of a population may or may not evolve in a given direction or at a given rate depending on the vagaries of the prevailing selection forces and the kind and amount of genetic variation immediately available to the population for response to changes in its environment. If over a period of time, most of the environmental change, and therefore, most of the evolution has been in a particular direction, i.e., if phyletic evolution has taken place, one can see with hindsight that a trend has resulted from this evolution. However, at each point along the trend it is impossible to predict where the next point will fall or if it will even fall in the general direction of the trend.

3.) Population-level trends in fossil species may be explained entirely by the sort of micro-evolutionary mechanisms known to be involved in the production of phyletic change in living species.

In the case of *P. vema*, phyletic evolution appears to have been the result of sporadic exertion of directional selection both for larger phenotypes and against smaller phenotypes and/or for diminution of stabilizing selection for smaller phenotypes; these three factors acted alone or in concert at different times.

If the intermittent occurrences of several warm-water radiolarian species observed by Hays and Opdyke (1967) and Bandy et al. (1971) between 1100 and 1710 cm really do indicate warmer conditions at depth, it is possible that the configuration of selection forces described above may have been at least in part related to periodic cooling of antarctic waters. There is evidence that Radiolaria inhabiting cold water tend to develop larger skeletons than members of the same species

living in warmer waters (Hays 1965). While the section of E14-8 between 1500 and 1100 cm does represent a cold period of major proportions according to paleotemperature estimates made by Bandy et al. (1971), bursts of rapid evolution in *P. vema* do not appear to be correlated in a consistent manner with secondary climatic fluctuations.

The relationship of rate of evolution to variation.—At first glance, the relationship of rate of evolution to variation in *P. vema* is somewhat perplexing. As stated above, the length of time required for a change of one standard deviation in a population mean (Table 2) was considerably smaller during the periods of rapid evolution than in the intervals between them. Simpson (1953) interpreted Haldane's (1949) statistic as a measure of how fast a population was "running through" the existing phenotypic variation which constituted its immediately available supply of raw material for evolution. If this interpretation is correct, one should expect to find that *P. vema* was least variable during times of rapid evolution and that the shape of the curve of the coefficient of variation vs. depth in core (Figure 5) would approximate the inverse of the width vs. depth curve. Instead, samples from the lower half of the range of *P. vema* are generally less variable than those from the upper half. These observations do not indicate that Haldane's statistic is useless so much as that its use is limited. The unspoken assumption made when this statistic is utilized is that if the rate of increase in width, for instance, is being measured, the width is increasing by elimination of smaller phenotypes from the population. This is precisely what happened in *P. vema* between 1600 and 1560 cm when phenotypes of less than 87 microns were almost entirely eliminated from the population (see Figure 6). The variation during this period of time was correspondingly low. But there are other ways in which the mean width of a population may be increased such as by addition of larger phenotypes with or without the removal of smaller ones, and these tend to increase the amount of variation in a population. Hence one finds high variation in *P. vema* between 1340 and 1280 cm and between 1145 and 1085 cm when phenotypes between 116 and 145 microns and between 145 and 174 microns, respectively, were being added to the population at a rapid rate. In general, the upper half of the range of

P. vema, which is characterized by the addition of wider phenotypes, is marked by a high level of variation while the lower half, which is characterized by elimination of narrower phenotypes, is marked by relatively low variation.

Extinction.—While it is true that the extinction of *P. vema* came at a time when this species was evolving rapidly, there is no reason to postulate hypertely or the notion “that somehow evolutionary momentum carries trends to inadaptable lengths and causes extinction” (Simpson 1953, p. 282) as the causative agent of extinction (Riedel 1971). Almost two million years previously, *P. vema* had been evolving even faster and did not become extinct. Furthermore, there is no evidence to support the notion that *P. vema* was ever evolving at a rate or in a direction which could not be commensurate with prevailing selection forces. At the time of its extinction, *P. vema* exhibited a fairly high amount of variation for thoracic width. The fact that *P. vema* was least variable for thoracic width during the Gilbert reversed epoch but did not become extinct until the beginning of the Matuyama, roughly a million years later, supports the contentions of Flessa, Powers and Cisne (1975) that “the degree of specialization is not an important determinant of evolutionary persistence” and that it is the *type*, rather than the degree of specialization that matters. At least, it appears that amount of variation had little relation to the extinction of *P. vema*.

Summary and Conclusions

1. A 50% increase in thoracic width over a period of approximately two million years was observed in the extinct radiolarian species *Pseudocubus vema* in deep-sea core E14-8 from the Antarctic.

2. The trend towards increased width in *P. vema* was “stepped” rather than straight, indicating a variable rather than constant rate of evolution.

3. Most of the observed morphologic change occurred during three relatively short bursts of rapid evolution preceded and/or followed by extended periods, three or four times as long as the bursts, during which the mean fluctuated between rather narrow limits.

4. Rates of change during periods of rapid evolution were 15 to 540 times greater than at other times. Proportional rates of change were

one to three orders of magnitude faster during the bursts of rapid change, and the amount of time required for the mean thoracic width of *P. vema* to increase by one standard deviation was one to three orders of magnitude longer in the intervals between the bursts than during them.

5. Observed changes in rates of morphologic change do not indicate gaps in the fossil record since there are no corresponding gaps in the magnetic stratigraphy of E14-8.

6. Variability for thoracic width was not necessarily related to rate of evolution. Variation was lowest when smaller phenotypes were being removed from the population without the addition of larger phenotypes. When larger phenotypes were added to the population, with or without the removal of smaller phenotypes, variation was high even during periods of rapid change.

7. The long-term trend towards greater thoracic width observed in *P. vema* clearly represents phyletic change.

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