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Tempo and mode of morphological evolution in three neogene diatom lineages

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TEMPO AND MODE OF MORPHOLOGICAL EVOLUTION IN THREE NEOGENE DIATOM LINEAGES

by

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Abstract

TEMPO AND MODE OF MORPHOLOGICAL EVOLUTION IN THREE NEOGENE DIATOM LINEAGES

by

ULF SORHANNUS

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Two late Pliocene planktic diatom morphotypes, Rhizosolenia praebergonii Mukhina and Rhizosolenia sigmoida Sorhannus, originated from Rhizosolenia bergonii Peragallo in the equatorial Pacific Ocean, after which R.praebergonii may have migrated into the Indian Ocean. An alternative interpretation is that R.praebergonii originated independently from R.bergonii in the Indian Ocean after which it underwent parallel evolution. The evolution of R.sigmoida was restricted to the eastern equatorial Pacific Ocean. Biotic factors in conjunction with paleoclimatic events may have played a role in the onset of the morphological divergence events between the lineages. A biometric analysis of the patterns of evolution indicates that both R.praebergonii and R.sigmoida underwent relatively rapid morphological change after their first appearances in the Pacific Ocean while R.bergonii evolved at a slower rate throughout the entire time period studied. As established morphotypes,which are morphologically distinct forms at a particular time level, R.praebergonii and R.sigmoida exhibit a slow down in the rate of

morphological change relative to the time period immediately after their first appearance. In the Indian Ocean the change in morphology of R.praebergonii proceeded much slower after its first appearance in relation to the Pacific Ocean cores. The morphological evolution of R.praebergonii in the Peru water mass seems to have been iterative (repetitive) with respect to R.sigmoida

Based on fitting a set of hierarchical linear models both R.praebergonii and R.sigmoida originated from R.bergonii in the Pacific Ocean through phyletic change in morphology possibly taking place at varying rates. To the contrary, if the first appearance of R.praebergonii in the Indian Ocean is a result of evolution as opposed to migration, it may be a case of punctuated character stasis which may reflect a speciation event. The relative frequency of character stasis is rather high in R.bergonii but also in R.praebergonii and R.sigmoida as they became established as distinct lineages in all the investigated sites. These observations are in agreement with the predictions of punctuated equilibrium hypothesis if the characters reflect species stasis.

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VIII. INTRODUCTION

Ever since Simpson published "Tempo and Mode in Evolution" in 1944 and "The Major Features of Evolution" in 1953 there has been a substantial amount of empirical and theoretical work, especially during the past ten years, done on rates and patterns of morphological evolution (e.g. Eldredge and Gould 1972; Kellogg 1975; Kellogg and Hays 1975; Gingerich 1976; Gould and Eldredge 1977; Bookstein et al. 1978; Malmgren and Kennett 1981; Hoffman 1982; Malmgren et al., 1983; Kellogg 1983; Hecht 1983; Levinton 1983; Lazarus et al. 1985;Hecht and Hoffman 1986; Lande 1986; Lazarus 1986; Levinton 1988; Kellogg 1988). Many of the investigations that followed Simpson's pioneering work in evolutionary paleontology directly utilized, as their basis, his methods, observations and ideas for further research. One of the major contentions of Simpson's treatise, which was largely based on statistical methods for interpreting the fossil record from an evolutionary point of view, was that morphological transformations within lineages proceed gradually through time (phyletic evolution) eventually giving rise to new species (speciation). His findings were both a contribution to and in agreement with Modern Synthesis which states that "all evolution is simply an accumulation of small genetic changes guided by natural selection and that transpecific evolution is

nothing but an extrapolation of events that take place within populations and species" (Mayr 1963). More importantly Simpson found that quantum bursts of evolution, which he in 1944 considered to be "preceded by inadaptive change" (pp.216-217) and in 1953 to be a "special case of phyletic evolution" (p.389), had taken place and that some lineages had remained unchanged during tens or hundreds of millions of years.

Eldredge and Gould (1972), who proposed the concept of punctuated equilibrium and later elaborated it further (Gould and Eldredge 1977), extended and refined the notion of quantum evolution, stating that evolutionary bursts are associated with the origin of new species in small allopatric populations through genetic revolution, as proposed by Mayr (1963), and that stasis within lineages was prevalent; thus refuting the importance of phyletic evolution in the speciation process as conceived by Simpson (1944,1953). In addition, the punctuated equilibrium, which then may be defined as a pattern of evolution where species stasis is punctuated by short stratigraphic intervals through which new species originate, asserts that the gaps in the fossil record are real and informative about rates of evolution. Consequently, it follows that the majority of lineages in the fossil record should reveal long periods of little or no morphological change punctuated by periods of rapid

change associated with lineage splitting or speciation. A second claim made by Gould and Eldredge (1977) and for instance Stanley (1975,1979) is that "speciation", the source of macroevolutionary variation, is qualitatively different from local adaptation within populations, thus requiring unique macroevolutionary mechanisms. Questions pertaining to the first claim or the strong version of punctuated equilibrium (Hecht and Hoffman 1986) can be investigated in the fossil record while the second claim cannot be subjected to rigorous paleontological testing. As a result of the reconsideration of Simpson's (1944,1953) original work on tempo and mode of morphological evolution, a debate over two extreme positions, phyletic gradualism and punctuated equilibrium, was triggered. Phyletic gradualism, which was Eldredge's and Gould's (1972) conception of gradual phyletic change, is a pattern of steady directional change in morphology resulting in the origination of new species.

Since quantification of morphological sequences in the fossil record form the basis for inferences about mode of evolution, which may be classified as being either punctuated,gradual,static or any sequential combination of the above, it is of great importance that certain criteria are fulfilled (e.g. Schopf 1982). Thus, in order to perform an analysis of the tempo and mode in

evolution over geologic time at least the following conditions should be met:

(1) One needs to find a lineage which has a relatively complete fossil record throughout its known temporal and geographic distribution range. This enables the worker to get large samples spaced at maximum stratigraphic resolution from separate populations and geographic regions for statistical treatments of both temporal and spatial variation.

(2) Since directional migration of geographic variants and species may confound or give rise to false local patterns of evolution it is necessary to have good time control of the stratigraphic sequences throughout the organism's distribution range. This facilitates evaluation of the presence of geographic variation (variants) and different morphotypes at a particular temporal horizon as well as possible directional migration of such.

(3) The most crucial criterion in a study of tempo and mode of evolution is that of species recognition. Since punctuated equilibrium and phyletic gradualism are patterns about the origination of new reproductive entities - as formulated by Eldredge and Gould (1972;Gould and Eldredge 1977) - we need a guide as to which fossil morphotypes are good biological species. For instance, what morphological traits available to

paleontologists reflect the biological species. This criterion is probably the most difficult to fulfill in the fossil record and consequently makes the testing of punctuated equilibrium using stratigraphic data ambiguous and virtually impossible - at least in the form punctuated equilibrium has been proposed by Eldredge and Gould.

The late Neogene and Quaternary microfossil record obtained from deep-sea cores is relatively complete and it allows for rather precise calibration of the stratigraphic sequences in absolute time due to the possibility of time-depth correlation using magnetostratigraphy. In addition, microfossils are abundant and diverse over a wide geographic region throughout their temporal range; this feature makes it possible to get large sample sizes for statistical treatment of morphological sequences in time and space. These unique characteristics of the deep-sea record also allow for the estimation of factors that may have obscured evolutionary patterns such as directional migration of geographic variants; thus fulfilling the first and second criteria mentioned above. The third criterion poses a problem for the entire fossil record as such and will be dealt with later on in this paper.

The purpose of this work is to undertake a study of the tempo and mode of character evolution in three

planktic Neogene diatom lineages and to relate periods of change and stasis in the investigated characters to environmental parameters. The quantification of morphological sequences through time and subsequent inferences about mode of character evolution was investigated by fitting a set of hierarchical linear models to the data. The conclusions about mode of change will be considered in the light of the null hypothesis of a random walk as well as by taking migration of geographic variants into consideration.

IX. PROBLEMS

The fossil record, especially the microfossil record, is unique in that it provides data on evolutionary and ecological processes over greater time scales than those available to neontologists. Consequently, the deep sea record cannot be ignored. On the other hand, the paleontological record also imposes restrictions on the types of problems that can be investigated with great confidence. This is largely due to the discontinuous nature of the preservation process and the difficulty of precise time correlation among localities (Jablonski et al 1986). Even though the deep sea record of shelled microplankton has turned out to be promising in documenting the speciation process (Berggren and Casey 1983) it still present some major difficulties

which I shall discuss in more detail.

A. Species recognition

One of the major obstacles in my work on diatom evolution is that of identifying "species"; this problem obviously depends on the type of species definition that is used. Since the hypothesis of punctuated equilibrium and much of evolutionary theory is phrased in terms of origination of biological species (Schopf 1982), defined by Mayr (1963) "as groups of actually or potentially inter-breeding populations in nature which are reproductively isolated from other such groups", it is imperative to examine the implications of using such a concept for my study of tempo and mode of morphological change in diatoms.

The utility of Mayr's nondimensional species concept is restricted only to sympatric populations at a particular instant in time. Species among Bacillariophyceae are primarily recognized by structural features of the silica shell, and it is not known to what extent these features reflect the genetic make up of the populations and thus biological species (Guillard and Kilham 1977). Many workers have shown that there is a large amount of genetic variability among clonal lines of diatoms that are morphologically similar (e.g. Murphy and Guillard 1976; Underhill 1977; Murphy and Belastock

1980). For instance, in an electrophoretic study of Skeletonema costatum populations Gallagher (1980,1982) demonstrated the occurrence of different winter and spring isomorphs with a genetic distance equivalent to that between different species of higher plants.

One of the taxonomic schemes proposed for classifying the living members of the genus Rhizosolenia relies on the configuration of the girdle bands (Gallagher, personal communication). Unfortunately, these traits are not preserved in the fossil record. However, there is a great deal of uncertainty in using shell morphology as a criterion for recognizing biospecies among present diatoms because it has been discovered that in some planktonic genera the cells of one species, studied in clonal cultures, produced the characteristic valve structures of more than one species (Guillard and Kilham 1977). Wood (1959) also reported that some large centric diatoms have dissimilar valves, each with the character of a different genus. In regions where the temperature is quite variable dimorphism and polymorphism has been encountered in several species of diatoms. For instance, Rhizosolenia hebetata and Rhizosolenia semispina have been found to be two forms of the same species rather than distinct species (Patrick and Reimer 1966 and references therein). The former is the Arctic morph and the latter the Atlantic form of the same

species. In addition, morphologically similar diatoms have been shown to be reproductively isolated and thus good biospecies (Mann 1984). Consequently, as also has been pointed out by Wood et al (1987), there are two major problems with recognizing biological species based on phenotypic information: firstly, the existence of cryptic sibling species may result in lumping of phenotypically similar but reproductively isolated groups; secondly, the difficulty of determining when intergroup morphological variability reflects reproductive isolation.

The utility of the biological species concept by Mayr (1963) for diatoms is also difficult due to the fact that some "species" reproduce only vegetatively - under such circumstances there exists no biological species (Bock 1986) - as opposed to the predominant mode of alternating between asexual and sexual reproduction. However, the extant Rhizosolenia bergonii Peragallo, which has been included in this study, is known to reproduce sexually since it forms auxospores (Cupp 1943). Consequently, it may be assumed that its presumed descendants also adopted the same mode of reproduction.

Considering the uncertainty of the investigated diatom lineages reflecting biospecies status at a particular temporal horizon, punctuated equilibrium will be restated in this study in terms of character evolution

and will be referred to as punctuated character stasis. Consequently, punctuated character stasis states that the fossil record reveals periods of no evolutionary change in characters or character complexes (stasis), punctuated by short periods of rapid change which may or may not be associated with the origination of new reproductively isolated entities. The above assertion differs from punctuated equilibrium presented by Eldredge and Gould (1972; Gould and Eldredge 1977) in that a punctuation does not necessarily in this case have to result in a speciation event nor does stasis have to imply species stasis. Moreover, the other extreme pattern or phyletic gradualism is studied in terms of phyletic character gradualism, which is a steady directional change in a character or character complexes that may or may not result in the formation of new species.

What really is or should be at stake here for the survival of the concept of punctuated equilibrium, as proposed by Eldredge and Gould (1972), is whether character punctuations leading to the origination of new species can be accounted for by microevolutionary mechanisms (see e.g. Lande 1986; Bock 1986; Hecht and Hoffman 1986; Kellogg 1988) or whether special macroevolutionary mechanisms have to be invoked for such events (e.g. Gould and Eldredge 1977; Stanley 1975,1979; Vrba and Eldredge 1985) . If character punctuations and

stasis can be explained by microevolutionary mechanisms, punctuated equilibrium is just an alternative way of saying "fast and no change". The microfossil record cannot directly provide answers to the inquiries about mechanisms. But it has a potential for indicating patterns of punctuations and stasis in traits which may require unique explanations in terms of mechanisms. In my work I have tested punctuated equilibrium and phyletic gradualism in terms of patterns of punctuated character stasis and character gradualism as stated above; this leaves the problems of mechanisms and recognition of biological species among the investigated diatoms open for interpretation and further research.

It is claimed in the literature (e.g. Ax 1984;Willmann 1985; see Lazarus 1983 for its application to microfossils) that the evolutionary species, which was defined by Simpson (1961) as " a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies", is the elementary units of evolution as if it could be recognized in an objective manner (Reif and Brettreif 1985). Many workers have pointed out that the evolutionary species definition is arbitrary due to the fact that there is no objective way to decide whether a particular species is the same at two points in time since reproductive continuity is not a valuable criterion

for this (e.g. Bock 1986; Reif and Brettreich 1985). According these authors, species can only be recognized nonarbitrarly in one time plane. Bock (1986) insists that the concept of "phyletic species" should be rejected as a theoretical species concept, while Reif and Brettreich (1985) introduce subjective criteria for demarcating evolutionary species. Due to the arbitrary nature of the "evolutionary species" as defined by Simpson (1961) and consequently the restricted utility it has in evolutionary theory (Bock 1986) the concept will not be used in this study. To the contrary, I will recognize lineages (ancestral-descendant sequences of populations) only in terms of morphological sequences through time. "Morphotypes", which is recognized based on morphological distinctness of two or more sympatric fossil populations, will be employed in this study to distinguish among morphological entities on a particular time level. However, in order to be able to determine the status of the investigated lineages as good biological species at various temporal horizons one needs information about morphological variability which characterizes extant sympatric Rhizosolenia biospecies.

B. Geographic/ecophenotypic variation

Both Gould and Eldredge (1977) and Bookstein et al (1978) emphasize geographic variation in studies of tempo

and mode of evolution because the presence of spatial variation in combination with directional migration will potentially obscure local patterns of temporal change in morphology. Consequently, such a phenomenon may give rise to false stasis, gradualism and punctuations in the investigated traits. This must be considered to be a substantial problem. Many workers have drawn their conclusions about tempo and mode based on data taken from a restricted area within the distribution range of a particular lineage (e.g. Kellogg 1975; Malmgren et al 1983; Gingerich 1976; Williamson 1981). Even though migration of morphological clines and geographic variants present an uncertainty in distinguishing "real" evolutionary patterns from spurious ones, the paleomagnetic reversal record, which permits world-wide synchronous time "slices" of the deep sea cores, enables us to get an estimate of geographic variation at different time levels. In my investigation I have included an analysis of geographic variation.

If there is a specific pattern of geographic variation present one has to be concerned about whether directional migration took place and the effects it might have had on temporal patterns of change in morphology. Immigration can be inferred by finding the time of the first appearances over the known distribution range and then comparing it to the presumed time of origination of

the lineage, that is where the earliest divergence event took place. If there turns out to be a stepwise directional pattern of first appearances, which can be determined to be significantly different within the limits of our resolution in at least three widely separated sites, migrational pathways can be inferred. After satisfactorily demonstrating directional migration the impacts of geographic variants on temporal evolution may or may not be substantial; this is, in my opinion, virtually impossible to show and will thus remain a problem to be taken into account when conclusions are drawn about tempo and mode of evolution. Bookstein et al.(1978) have pointed out that a relative increase in the character variances at consecutive time levels, in addition to bimodal/multimodal frequency distributions, are expected in sites affected by directional movement of geographic variants, assuming no change in morphology during migration. The above approach suggested by Bookstein et al (1978) is not sufficiently conclusive due to the fact that a temporal increment in character variances and the presence of bimodal/multimodal frequency distributions may be a result of other phenomena such as the origination of polymorphism, sediment mixing, relaxation of the selection pressure and/or aggregation in conjunction with directional evolution or any combination of the above.

C. The stratigraphic record

Studies on tempo and mode in evolution utilize data extracted from the fossil record which is generally incomplete. This presents problems with interpreting morphological sequences and may in some cases lead to erroneous conclusions. The presence of gaps may obscure gradual evolution and give rise to a false impression of a punctuated event (e.g. Bookstein et al 1978; Levinton and Simon 1980). For instance, Raup and Crick (1982) discovered in their analysis of character evolution in Kosmoceras that gaps in morphology are associated with sedimentary breaks more often than expected by chance although the majority of discontinuous sediments are not linked to gaps in morphology. The existence of gaps in the fossil record may be a result of missing sediments (Schindel 1980,1982; Dingus and Sadler 1982) which is the outcome of the discontinuous nature of the sedimentation process, that is non-preservation and/or non-deposition of fossil material. Additionally, Schindel (1982) pointed out that "most profound breaks" should be interpreted as periods during which the habitat deteriorated resulting in migration and subsequent recolonization at the return of hospitable conditions. Methods for assessing the completeness of stratigraphic sections at a particular level of resolution have been developed in order to

evaluate results of studies of tempo and mode of evolution (Sadler 1981; Dingus and Sadler 1982; Schindel 1982). Even though these methods are rather crude, Mckinney and Schoch (1983) have demonstrated that failure to use them may give rise to misinterpretations of data. Due to the discontinuous nature of fossiliferous sediments many workers (e.g. van Andel 1981) have questioned the reliability of evolutionary patterns that are derived from the record. This is one of the most serious limitations imposed by the stratigraphic record on studies concerned with tempo and mode. However, Dingus and Sadler (1982) pointed out that testing of neontological concepts in the biostratigraphic record requires organisms with a dense fossil record, long generation times and sections which are fairly recent and have high rates of sediment accumulation. Unfortunately, diatoms have a relatively short generation time but otherwise they fulfill the above requirements. Sampling and resampling of the same population in different places, if possible, gives confidence to the data if patterns are "similar" in all the localities.

Another major problem, which is encountered when using stratigraphic data in evolutionary studies, is that of aggregation of fossils resulting in accumulation of many thousands of generations into a particular stratum. Levinton and Simon (1980) indicated that the phenomenon

of aggregation tends to obscure short-time trends as well as evolutionary patterns in general. Similarly, Bookstein et al (1978) discussed the problem of inferring gradual, punctuated mode of change and stasis from data pooled over several thousand generations. According to Bookstein et al (1978) hidden randomness in data increases as a function of aggregation, and the hypothesis of punctuated equilibrium should not be applied to highly aggregated data. Gradualism may be demonstrated with confidence in situations where a series of samples with overlapping frequency distributions and with rather constant variance show directed change (Bookstein et al. 1978). Likewise, stasis cannot be inferred unambiguously based on highly aggregated fossil data. For instance, a morphological sequence, that first appears to be in stasis, may be taken for a gradual trend as a longer time span is sampled (Bookstein et al 1978). Mixing of marine sediments by burrowing organisms as well as by diagenetic (compaction) and environmental factors (rate of sedimentation and the turbulence level) influence the vertical position of fossils and are among the primary causes of time-averaged fossiliferous sediments, especially in shallow shelf deposits (Fursich 1978). Diatoms generally have a short generation time, ranging from 4.4 hours in small forms to 24 hours in very large species (Werner 1977); this will give rise to highly

aggregated assemblages since the fossils are not preserved at such a fine scale of resolution. Consequently, if the rate of evolution is properly measured as change from one generation to another (Bookstein et al 1978), inferences made about mode of evolution in diatoms may be unreliable. An additional difficulty in conjunction with aggregation, which specifically pertains to diatoms, is ontogenetic variation. Since most diatom species go through size diminution as they divide asexually. This produces false patterns of change, especially in a situation of differential preservation of cell sizes at separate points in time.

The paleomagnetic reversal record, which has been dated independently of the organisms through radiometric techniques, forms the basis for constructing the time axis in my study. The major drawback with this procedure is that the temporal horizon of samples located between the magnetic reversals is calculated through linear interpolation without considering variation in the sedimentation rate. Consequently, the exact temporal position of such samples must be interpreted with caution.

D. Quantification of morphological sequences

Bookstein (1987;personal communication) points out

that in studies of tempo and mode in evolution the null hypothesis of a random walk, which is the "simplest" explanation for a temporal sequence of means, must be rejected before "rates" of evolution can be "measured". The reason for this is that there exists no underlying forcing function if the null hypothesis is accepted but only a step variance. The step variance is the variability in step size between the successive means of a sampled time sequence which is a result of a random walk. From a purely mathematical point of view "an evolutionary rate is a derivative of some quantitative feature with respect to time and such derivatives don't exist for random walks" (Bookstein, 1987). Since a random walk may imitate trends,punctuations and stasis in characters, we are always faced with the null hypothesis as an alternative explanation for a temporal sequence of morphological changes. Bookstein (1987;in press) has developed a statistical test (Range Test) which can distinguish trends,punctuations and stasis in characters due to random walks from those that are nonrandom. The question that arises when the null hypothesis is accepted is whether the observed pattern was generated by random or deterministic processes since a random walk does not always imply random morphological changes in a population per se (Fisher 1986); in fact the changes may very well be deterministic but the "causal" factor(s) may vary

randomly. Moreover, Bookstein's suggestions must be interpreted within a biological framework since populations of organisms must be "functional" in their environment and are thus ultimately restricted as to what is possible as far as morphology is concerned at a particular point in time. In other words a biological system cannot be truly random in the sense of a sequence of coin flips but it may very well be random within "restrictive boundaries". For instance, Raup and Crick (1981) discussed a model in which a random walk occurs within selective boundaries and Hecht (pers.comm.) suggested that the same phenomenon may take place within developmental boundaries. Since inferences about random morphological variation present in temporal and spatial fossiliferous sequences seems to be a controversial issue it will present a problem in interpreting morphological sequences in the fossil record. Nevertheless, in my work I will use the Range Test developed by Bookstein (1987) for evaluating the validity of the null hypothesis of random walk for explaining the time series.

Many investigations on tempo and mode of morphological evolution have been performed without any quantitative definition of punctuated equilibrium,stasis and phyletic gradualism (e.g. Gingerich 1974,1976;Kellogg 1975;Ozawa 1975;Williamson 1981). Consequently, one worker's punctuated equilibrium has been another person's

phyletic gradualism (e.g. Gould and Eldredge 1977 and their interpretation of Kellogg's and Gingerich's data) and vice versa. In order to test for the presence of punctuated equilibrium, phyletic gradualism and stasis as patterns of character evolution, we need a "rule of thumb" to follow in order to avoid chaos. For instance, Gould (1982) defined "geologically instantaneous" as 1 percent or less of later existence in stasis. The problem with this is that lineages characterized by long duration will be more prone to show punctuated patterns than the ones with relatively short temporal distributions. Moreover Gould (1982) did not explain the exact meaning of stasis from a quantitative point of view. An alternative approach was taken by Bookstein et al (1978) who defined punctuated equilibrium, phyletic gradualism and stasis from a statistical point of view. Thus, instead of testing either model they proposed to estimate jointly the comparative contribution of punctuated change, phyletic gradual change and stasis in a character or any combinations of the above to explaining the variance in the data. This can be done by fitting a set of hierarchical linear models, which describe gradual phyletic and punctuated change as well as stasis or any admixture of these, to the "raw" data through linear regression techniques. Another quantitative definition of morphological equilibrium and punctuation was proposed by

Lande (1986) who adopted Simpson's (1961) and Mayr s (1969) taxonomic recognition of subspecies or the "75% rule" of overlap as a criterion. Thus, "the duration of stasis for a particular character in a fossil sequence is defined as the maximum period in which the mean phenotype remains within subspecific bounds, i.e., mean phenotypic changes by less than two phenotypic standard deviations measured within populations" (Lande 1986). Similarly, "a punctuational event could be defined as a discontinuity of at least this magnitude, that is, a change in the average phenotype by more than two phenotypic standard deviations between successive samples (or within a geologically very short time)" (Lande 1986). Since Simpson's (1961) and Mayr's work mostly deals with vertebrate taxonomy, for which also the "75% rule" was derived, it may not be appropriate to use such an approach in my study since it is not known to what extent the rule applies to protistans such as diatoms. Cheetham (1986) proposed an operational distinction between gradual and punctuated patterns. The former would be adopted in situations where intraspecific morphological changes are sufficient to account for interspecific changes while the latter requires that differences across species boundaries cannot be explained in terms of changes within species. This methodology is biased towards a lower than actual rate of evolution which

according to Cheetham (1986) would make punctuations more convincing. Moreover, Cheethams approach cannot be used in my study since it requires that the time of first appearance of the ancestral lineage is known, which is not the case, and that it has been sampled throughout its entire temporal range. The statistical technique presented by Bookstein et al (1978) for testing one linear representation of the data in the light of other such models is employed in my study of the tempo and mode in evolution since the advantage of this procedure is that it makes it to classify a morphological sequence objectively as being either static,gradual or punctuated or any admixture of the above. However, fitting the hierarchical linear models should be regarded as a first approximation for interpreting the data.

There is a large literature (e.g. Cheetham 1986; Raup and Crick 1981; Bookstein et al 1978; Bookstein in press; Charlesworth 1984) which deals with the methodological difficulties of quantifying morphological sequences in the fossil record (reviewed by Fenster and Sorhannus, unpublished). In general, there have been two main approaches to quantification of temporal metric data; those that use various regression techniques (e.g. Bookstein et al 1978) versus those that calculate a mean rate of change between two morphological mean values separated in time (e.g. Charlesworth 1984; Cheetham

1986). Temporal variation in morphology is, as pointed out by Bookstein et al (1978), composed of an admixture of evolutionary change and sampling error in unknown proportions and thus should be modeled either as a series of trends or equilibria. In detecting the presence or absence of anagenetic change one would have to fit to the data a set of hierarchial linear models through piecewise linear regression and find the model that explains most variance with the fewest number of parameters. These models simply ignore nonlinearities, thus assuming that non-zero rates are constant. According to Bookstein (1975) nonlinear data may be fitted through polynomial regression. However, such a technique is not desirable since it brings about drawbacks, such as "susceptibility to systematic regional biases, faulty behavior at the limits of the predictor range and the creation of artificial mathematical features (extrema,points of inflection)" (Bookstein 1975). To the contrary, piecewise linear regression requires that the worker detects "nodes" in the data where the trend appears to bend. The position of these "nodes" may be inferred by visually inspecting the distribution of the data (see Bookstein, 1975). Thus, a morphological time series characterized by sections with distinct directions of change justifies a subdivision of a sequence into subseries between which the "nodes" exist (Bookstein, 1975). Studies in which the

mean and usually the variance of the rate of evolution are estimated, the changes in the population mean through time are assumed to reflect strictly evolutionary change, in the sense of temporal genetic change in the population (e.g. Charlesworth 1984;Cheetham 1986). In fact, this assumption is probably violated all the time since fluctuations in mean morphology through time may be attributable to biased sampling,differential temporal preservation, measurement error and ecophenotypic change. In my investigation I have adopted the approach of Bookstein et al (1978) to quantifying morphological sequences in the fossil record since it does not make any assumptions about the type of change (genetic versus nongenetic) that take place between successive temporal horizons; it just detects trends and stasis which may be subject to interpretations.

The utility of multivariate versus univariate methods in studies of morphological variation in time and space has been discussed. For instance,Simpson (1953) stated that it would be preferable to quantify trends in overall morphology rather than in single characters since such an approach would be more representative of the evolution of species; he suggested that the methodology of discriminant functions developed by Fisher might be a way to approach the problem. Similarly, Willig et al (1986) concluded that morphometric variation in natural

populations should be investigated by multivariate techniques because such an analysis take correlation among characters into consideration as opposed to univariate techniques. Consequently, little correspondence was detected in the outcome of an analysis of geographic variation of morphometric data (22 mensural characters) in 27 Brazilian bat species using MANOVA and ANOVA (Willig et al 1986). Cheetham (1987) undertook an empirical study of how perceived patterns of evolution are affected by the use of single characters (46 characters) versus overall morphology in closely spaced sequential populations of nine Neogene bryozoan Metrarabdotus species. The results from Cheetham's (1987) work also suggest that interpretations of patterns of change in single characters in isolation should be made with caution since none of the single characters trends in the nine species were sufficient to modify the punctuated pattern in overall morphology which characterized the evolution within the genus Metrarabdotus. In my study there seems to be close correspondence between the outcome of the multivariate and univariate analysis of three morphometric characters probably due to the fact that two of the three traits, which have similar univariate patterns, dominate the total canonical structure (Sorhannus et al,in press). Moreover, the correlation between the three traits is low

and not significant on 5% significance level. In this case a multivariate approach appears not to contribute much additional information about tempo and mode of evolution and is not necessarily indispensable for the analysis.

X. MATERIAL AND METHODS

A. Temporal and geographic distribution of Rhizosolenia

One of the lineages I have examined in my study of tempo and mode is the fossil form Rhizosolenia praebergonii Mukhina - a centric diatom, which belongs to the family Rhizosoleniaceae, - which is widely used for biostratigraphic correlation in upper Pliocene and lower Pleistocene sediments of the equatorial Pacific and Indian Ocean (Mukhina 1965,1969; Burckle and Opdyke 1977; Burckle 1972,1978a; Sancetta 1982; Barron 1985). The Neogene geographic distribution range also incorporated the northwest Pacific (Koizumi 1968; Koizumi and Tanimura 1985), the north Atlantic (Schrader 1977; Baldauf 1984) as well as the equatorial and subtropical Atlantic Ocean (Fourtanier, Sancetta personal communication). The first appearance of R.praebergonii in the equatorial Pacific Ocean in the middle of the Gauss Chron at 3.1 Ma before present and it disappeared in early Pleistocene near the middle of the Olduvai Subchron or 1.6 Ma (Burckle and

Trainer 1979). In higher latitudes of the Pacific Ocean the temporal distribution range become progressively shorter, the first appearance datum levels ranging from upper Gauss to lower Matuyama (approx. 2.7 - 2.3 Ma) and the last appearance from lower Matuyama Chron to just above the Olduvai event (approx. 2.2 - 1.6 Ma) (Burckle et al 1985). In the equatorial Indian Ocean R.praebergonii appeared later than in the equatorial Pacific Ocean; in upper Kaena Subchron (approx. 2.9 Ma) (Burckle and Opdyke 1977).

Another lineage, which was discovered and described as Rhizosolenia sigmoida Sorhannus (submitted) seems to have been confined to the eastern equatorial region of the Pacific Ocean or the Peru water mass during a short period of time in upper Pliocene, approximately between 3.4 - 3.0 Ma or from lower Gauss Chron to lower Kaena Subchron. This is also a centric diatom, to date found only in the fossil record, and it belongs to the family Rhizosoleniaceae.

Rhizosolenia bergonii Peragallo, which is an extant diatom species among Rhizosoleniaceae with a relatively good fossil record, is included in this analysis because it is thought to be the ancestral form of the previously discussed lineages. This is a relatively large diatom species which rarely shows high abundances in modern diatom assemblages (Guillard and Kilham 1977) and it also

seems to fluctuate in abundance in the fossil record. Both at present and in the past R.bergonii has been characterized by having a geographic distribution range incorporating the tropical and subtropical regions of the Pacific,Indian and Atlantic Ocean (e.g. Guillard and Kilham 1977; Cupp 1943). The temporal distribution range extends from early Miocene to present (Burckle, personal communication).

These three lineages are relatively abundant over a wide geographic region throughout their known temporal range which permits statistical analysis of trends.

B. Morphological variables studied

Permanent slides were prepared after the method of Schrader (1974). The sampling interval in this study ranged from 10 cm to 1 m. Due to the discontinuous nature of the sedimentation process, the samples are not evenly distributed in time; where possible, the minimum sample spacing is on the order of 0.03 m.y. while the maximum spacing is approximately 0.3 m.y.. Core samples, which ranged from 1 cc to 2 cc in volume; thus averaging 0.003 m.y. of sediment, were broken down in 10% HCL to remove $CaCO_3$ and organic material. Each sample went through a series of six washes with distilled water at 90 minute intervals after which 3-5 drops of the residue were pipetted onto a coverslip. When the water had evaporated

- a process that was speeded up by putting the coverslip onto a moderately heated plate - the coverslip was fixed onto a microscope slide by using Permount. Before the samples were studied the compound was allowed to dry for a couple of days.

At each investigated site approximately 30 specimens per sample were measured and on each specimen the following measurements were taken with an ocular micrometer at a magnification of 1000X: (1) length of apical process (AL), (2) width of the valve 8 microns below its apex (WC) and (3) height of the hyaline area at the apex of the valve (HH) (fig. 1). Since one micrometer unit equals 0.4 microns in this study the variables were measured to the closest 0.4 microns and analyzed on the C.U.N.Y. mainframe computer using the software package SAS (version 5, 1985). Although the choice of variables may seem somewhat arbitrary, it was largely dictated by the preserved condition of the valves of the three Rhizosolenia lineages (fig. 1). In all cases, the middle part of the frustule has been broken off and the complete shell has never been recovered, except for the extant R.bergonii.

C. The cores

The investigated lineages were recovered from Deep Sea Drilling Project (DSDP) and Lamont - Doherty

Geological Observatory (L-DGO) cores, which have been taken from all
parts of the oceans. The coverage of the world ocean by deep sea cores is complete in the sense that all biotic provinces are represented. In piston cores as opposed to rotary cores the Earth's paleomagnetic reversal record can be identified and tied to an absolute time scale; this is done by correlating the polarity sequence of the deep sea core to terrestrial volcanic rocks in which the reversal events have been dated through the potassium-argon method. Sites, that produced rotary cores, that lack a reliable magnetic record can be tied to cores for which absolute dates are available, through oxygen isotope and calcium carbonate data as well as biostratigraphic markers. Each magnetic reversal is a globally synchronous event which makes correlation between sites far away from each other possible and more reliable. The temporal position for samples located between magnetic reversals was calculated through linear interpolation using the revised geomagnetic time scale of Berggren et al (1983). Thus, the construction of the temporal axis in this investigation assumes a constant sedimentation rate. Marine cores generally have a continuous sedimentation (see figures 2-8 for relationships between depth and time at the sites studied) allowing samples to be taken from a continuous

but time - averaged fossil record.

The deep sea cores that have been used in this study (fig 9-10) were chosen based on several criteria, such as the presence of a good paleomagnetic reversal and stable isotope record as well as the abundance of the investigated lineages throughout their known geographic and temporal distribution range. Moreover, several sites were purposely selected within the same water masses rather close to each other which facilitates comparisons of patterns of evolution among locations (fig. 10). The Atlantic cores were omitted in this study since the investigated lineages have a poor fossil record in that part of their distribution range. Consequently, all the deep sea sections considered are located in the equatorial upwelling zone of the Indian and Pacific Ocean which are characterized by having a relatively good Neogene and Quaternary microfossil record and time control.

DSDP Site 504, which is the easternmost core of the equatorial Pacific Ocean in this study, is located at 1° 13,6'N and 83° 43,9' W (fig. 9-10). The core was taken from the Panama Basin, south of the Costa Rica Rift (Sancetta 1982) and can be considered to be either below the Peru water mass or between the equatorial and Peru water masses (fig.10). Since there are no paleomagnetic data directly available at this particular site it was

dated by adopting diatom zones and datum levels as well as paleomagnetic correlations from Burckle (1972,1977,1978b;Burckle and Trainer 1979;Burckle et al 1978) (Sancetta 1982). This is possible since most of the datum levels have been confirmed to be isochronous throughout the equatorial Pacific (Burckle 1978b). The average sedimentation rate of DSDP site 504 has been estimated by Sancetta (1982) as 50 m/m.y. which is relatively high.

A DSDP site located within the Peru water mass (1° 45'S; 85° 54'W) but further south and west of DSDP core 504 is Site 157 (fig 9-10). Since this core was obtained by rotary drilling from the southern edge of the Panama Basin on the Carnege Ridge there is no paleomagnetic reversal record available. Consequently, the temporal position of the samples from Site 157 is arrived upon through correlation of this core with the central Pacific sites (RC12-66 and DSDP Site 573 which have good magnetostratigraphy) by means of chemostratigraphy (calcium carbonate concentration) and various biostratigraphic indicators (Burckle 1978a). The average sedimentation rate of this site throughout the temporal scope considered was approximately 76 m/m.y. which is relatively high in comparison to the central Pacific sites.

A core, which is also closely associated with the

Peru water mass even though it is within of the central equatorial Pacific upwelling zone, is DSDP Site 572C; this site is an intermediate (1° 26' N; 83° 43,9' W) on an east-west transect between the central equatorial and eastern equatorial cores (fig.9-10). Since the chronology of magnetic reversals is not directly available in this deep sea section the dating at Site 572c has been done through correlation with the paleomagnetics in L-DGO core V28-179 and DSDP Site 573 in the central Pacific using calcium carbonate concentration (Prell 1985). This site has a moderate sedimentation rate for the time duration considered in this study,that is an average rate of approximately 16 m/m.y..

DSDP Site 573 was taken from beneath the central equatorial water mass (0° 29'N; 133° 18'W) of the Pacific upwelling system (fig 9-10). Paleomagnetic data is directly available because Site 573 is a hydraulic piston core;thus the dates are generated directly from the revised geomagnetic time scale of Berggren et al (1983). The average sedimentation rate of the late Pliocene and early Pleistocene sections is 14.5 m/m.y. which is lower than the rates in the easternmost sites.

Both V28-179 (4° 37'N: 139° 36 W) and RC12-66 (2° 36'N; 148° 12'W) are L-DGO cores, which are located to the northwest of DSDP Site 573 in the equatorial watermass, not far apart from each other (fig.9-10). In

these hydraulic piston cores a good isotope and magnetic record has been recovered and has been worked out by Shackleton and Opdyke (1977) for V28-179 and Foster and Opdyke (1970) for RC12-66; the absolute time of the reversals were adopted from the Berggren et al (1983) time scale. The average sedimentation rate was rather low for both V28-179 and RC12-66 throughout the sampled section, approximately 3 m/m.y. for both cores.

The westernmost sites considered in my investigation were the L-DGO cores V29-40 (10° 29'S;78° 3' E) and RC14-22 (11° 27'S; 75° 8.9'E) from the equatorial upwelling region of the Indian Ocean (fig. 9-10). The paleomagnetic and biostratigraphic data for both V29-40 and RC14-22 sites have been reported by Burckle and Opdyke (1977). The time axis was generated from the Berggren et al (1983) revised geomagnetic time scale. Since a large portion of V29-40 is missing across the Pliocene/ Pleistocene boundary, RC14-22 was chosen to cover this part of the temporal distribution range of R.praebergonii and R.bergonii. Due to the fact that these cores are located close to each other (fig.9-10) the data have been combined into a single section as if it were collected from the same site; thus in V29-40 R.praebergonii and R.bergonii were sampled from the Upper Mammoth Subchron to the Matuyama/Gauss boundary and in RC14-22 from the Matuyama/Gauss boundary up to the Lower

Olduvai Subchron. The average sedimentation rate for both cores was of the same magnitude as in the central Pacific sites or 4 m/m.y. for V29-40 and 4 m/m.y. for RC14-22.

XI. ANALYSIS

The measurement error for each variable was determined by measuring the same specimen 20 times at two separate times after which the data were analyzed by an ANOVA procedure and a Tukey's studentized range test. The length of the apical process (AL),the width of the valve (WC) and the height of the hyaline area (HH) form the basis for the investigation; all these variables have a measurement error of approximately 0.0632 microns ($P>0.05$). In addition, the covariance matrices of the three variables for each lineage are of full rank or in this case 3; this implies that the measurements are not redundant, that is they are not linear combinations of each other. However, there are six samples of R.praebergonii from DSDP site 157 which are not of full rank or 2. These six samples show no variability in HH throughout the time interval ranging from 2.75 to 2.43 Ma. Moreover, there is generally low correlation between the investigated characters in the three lineages; the correlation coefficient ranges from - 0.01 to 0.5 which is not significant at the 0.05 level. Consequently, AL,WC

and HH can be considered to be three independently changing characteristics.

A. The univariate patterns

The pattern of evolution of the mean apical process (AL) and the mean height of the hyaline area (HH) in R.praebergonii in the central equatorial Pacific sites is characterized by an initial period of rapid change (3.1 - 2.7 Ma) followed by a period of time during which the value of these variables remained essentially unchanged (2.7-1.7 Ma) (fig.11-14,20-23). This trend also fits the temporal transformation of HH in Site 157 in the eastern equatorial Pacific (fig.24). To the contrary, both AL and HH of R.praebergonii in the Indian Ocean and AL of the same lineage in the eastern equatorial Pacific core do not indicate any time intervals designated by different direction and rate of change (fig. 15;fig.19,25). However, the evolution of AL in the eastern equatorial Pacific appears to have taken place at a faster pace than in the Indian Ocean. As far as the mean width of the valve (WC) in R.praebergonii is concerned it seems to have become slightly larger in younger sections; this is particularly evident in the Indian Ocean core,RC12-66, Site 573 and maybe Site 572C while Site 157 indicates a small decrease in the mean width (fig.29-33,34,38).In the other central Pacific site, that is V28-179, the valve

width fluctuated within the same broad range of variability throughout the investigated time interval (fig. 33).

On the other hand, R.bergonii remained relatively unchanged throughout the whole time interval sampled with regard to all the three traits under consideration in this study (fig.11,13,15,17,19;fig.21-25,27;fig.30,32,34-35,38). Moreover, no apparent differences seem to have existed between the cores even though they are fairly distant in space.

The mean AL of R.sigmoida changed in a fashion similar to that of R.praebergonii, that is an initial rapid phase (3.3 - 3.15 Ma) followed by a time period characterized by little or no change (3.15-3.0 Ma) (fig. 16-17). Similarly, the mean width of the valve showed an accelerated pace of change during the first 400,000 years of the existence of R.sigmoida after which it slowed down as opposed to R.praebergonii (fig.35-36). Such a discrepancy in the rate of evolution cannot be observed in the mean HH which seems to indicate a steady directional pattern of change (fig. 26-27). If the three variables of R.sigmoida and R.praebergonii are compared through time in Site 157 it is noticeable that they show an iterative pattern of change, that is the latter essentially repeating the morphological transformations observed in the former (fig. 18,28,37).

B. Ancestor - descendant relationships

The use and importance of paleontological versus neontological data in reconstructing phylogenies has been, and still is, a celebrated issue in systematics (e.g. Schaeffer et al 1972; Cracraft and Eldredge 1979; Lazarus and Prothero 1984). The debate has primarily been in reference to the vertebrate and macroinvertebrate fossil records. According to Lazarus and Prothero (1984) most deep sea microfossils lack a sufficient number of hierarchically nested sets of characters and show frequent convergences as well as iterative evolution, which is a temporally repetitive pattern of evolution, thus making complex phylogenetic inferential methods ineffective. Since iterative evolution occurred in the investigated lineages (fig. 18,28,37) and due to the limited number of characters used in this study a cladistic approach to inferring the evolutionary relationships would be unreliable according to the principles outlined by Lazarus and Prothero (1984 and references therein). On the other hand, our stratigraphic data seem to fulfill the criteria for reliability (Lazarus and Prothero 1984) since the morphological sequence of Rhizosolenia lineage is found in the same temporal order in all the investigated localities; there is also good geographic control and preservation of the

examined lineages. Therefore, ancestor-descendant relationships between R.praebergonii and R.bergonii as well as between R.sigmoida and R.bergonii should be interpreted by close sampling, rather than through a cladistic approach, of temporally separated populations. Such sampling is made possible by the high quality of the deep - sea stratigraphic record. However, this approach requires three assumptions: (1) the direct ancestor has been preserved, (2) the direct ancestor will be included in the samples and (3) morphological data, which delimit phena, are appropriate for phylogenetic analysis. As pointed out by Prothero and Lazarus (1980), given these assumptions, ancestors can be recognized when the hypothetical ancestor can be inferred to be older than its descendant and when all possible ancestral populations are sampled. This converts the problem of the recognition of ancestors to a problem of sampling. Through the efforts of various deep-sea drilling programs there are now a large number of sites available that cover a broad geographic area. Thus, it is possible to sample most of the potential ancestral populations as well as descendant lineages through time over their geographic range. Moreover, the chronostratigraphy of many of these sites can be reliably determined by three independent correlative methods: biostratigraphy, chemostratigraphy and magnetostratigraphy. In addition,

radiometric dating of magnetostratigraphy makes possible the calibration of evolutionary events in absolute time as well as positioning of samples in time.

Given this reasoning, the potential ancestral-descendant relationships between R.praebergonii and R.bergonii were investigated through sampling rather closely spaced temporal populations. R.praebergonii primarily occurred in the equatorial region of the Pacific, Atlantic and Indian Ocean and it first appeared in the equatorial Pacific in the middle of the Gauss Magnetic Chron as a transitional form (Burckle and Trainer 1979). However, it appeared in the Indian Ocean 200.000 years later as a distinct form. Consequently, the ancestor-descendant analysis was restricted to the equatorial Pacific region of its geographic range ensuring that all possible ancestral populations were sampled. R.praebergonii was morphologically closer to R.bergonii than to any other Rhizosolenia lineage present at its first appearance in the five examined locations (fig.11,21;fig.30,32,34) which supports the existence of phylogenetic affinity between the two lineages. Moreover, an evolutionary relationship between these two lineages is supported on their relative temporal positions in the stratigraphic record; that is R.bergonii occurred prior to,during and after the origination of R.praebergonii. In addition, after the first appearance AL and HH of

R.praebergonii started to diverge substantially from the presumed ancestral form while WC did not indicate such a sharp separation from R.bergonii (fig.11,21;fig. 30,32,34). Based on the above arguments, it can be concluded that R.praebergonii originated from R.bergonii in the equatorial region of the Pacific Ocean and more importantly that the criteria presented in Prothero and Lazarus (1980) for testing the hypothesis of an ancestral-descendant relationship have been satisfied. Based on similar criteria as above, R.praebergonii may also have evolved from R.bergonii in the Indian Ocean since it appeared there 200,000 years earlier as a distinct form as compared with the Pacific Ocean; however the intermediate forms are lacking in the Indian Ocean (Fig. 19,25,38).

Likewise, the ancestral-descendant relationships between R.sigmoida and R.bergonii can be investigated since the latter occurred prior to, during and after the time of first appearance of the former. Moreover, R.sigmoida seems to have been endemic to the Peru water mass throughout its temporal range; consequently the origination of the lineage most likely took place in that particular region and thus the sampling of all possible ancestral populations was confined to DSDP Sites 157 and 504 (fig. 9-10). In this case R.sigmoida was also morphologically closer to R.bergonii than to any other

Rhizosolenia lineage around the time of its first appearance (fig.16-17;fig.26-27;fig.35-36). After the first appearance, AL,HH and WC of R.sigmoida started to diverge sharply from the presumed ancestral form of R.bergonii till it became established as a distinct lineage (fig.16-17;fig.26-27;fig.35-36). Based on the criteria of Prothero and Lazarus (1980) for inferring ancestral-descendant relationships it can be concluded that R.sigmoida evolved from R.bergonii in the eastern Pacific Ocean.

C. Rates of morphological change

The rates of change in the mean length of the apical process (AL),the mean width of the valve (WC) and the mean height of the hyaline area (HH) were analyzed by simple linear regression (slope), the F-test and the T-test (Zar 1984; Sokal and Rohlf 1981) using SAS GLM (SAS USER GUIDE:Statistics, version 5 1985). Where the time series of AL,HH and WC indicated a "significant bend", which was determined by visually inspecting the data, the sequence was divided and the subsections were examined separately by regression analysis and compared for significant differences in rates of change (slope) by using the F-test. The regression approach looks for long term trends as well as absence of trends in mean morphology through time; thus ignoring fluctuations which

may be due to minor environmental perturbations and sampling error (Lande 1986). By using Student's t-statistic the null hypothesis that states that the regression slope is equal to zero, was tested (Zar 1984;Sokal and Rohlf 1981).

The temporal change in the mean length of the apical process in R.praebergonii indicates a shift in direction and a rate slow down, beginning near 2.7 Ma in the central equatorial sites (RC12-66, V28-179, DSDP 573 and DSDP 572C) (fig. 12-13;table 1); this is primarily supported by the fact that in three out (RC12-66,DSDP 573 and DSDP 572C) of the four cores the regression slopes were significantly different before and after the inflection point at 2.7 Ma. The rate slow down and the change in direction after 2.7 Ma does not necessarily mean that the slope is equal to zero; this hypothesis was rejected only in Sites 572C and RC12-66 at the 0.05 significance level (table 1). Prior to 2.7 Ma the slopes deviate significantly from zero in all the central equatorial sites. Only V28-179 did not indicate a rate discrepancy (table 1) before and after the 2.7 Ma time level. Consequently, the shift in both direction and rate of change in AL at 2.7 Ma justifies dividing up the temporal sequence into two main stages; a phase characterized by a rapid directional rate of change, during the time period R.praebergonii diverged from

R.bergonii (3.1 - 2.7 Ma) followed by a period of a relatively slower rate (2.7 - 1.7 Ma). In Site 157 and in the Indian Ocean core the evolution in the mean apical process length of R.praebergonii does not suggest any shifts in direction and rate of evolution (fig. 15,19). However, the calculated regression slopes in the Indian Ocean and the eastern Pacific equatorial sites are different from each other; the former indicating no or little net change through time since the null hypothesis of no change was not rejected (P>0.05) while the latter showed directed change (fig. 15,19;table 34).

The height of the hyaline area (HH) in R.praebergonii also shows a shift in the direction and rate of change at 2.7 Ma in the central equatorial sites (RC12-66,V28-179,DSDP 573,DSDP 572C) as well as in the eastern equatorial site (DSDP 157) (fig. 20-24;table 2). The above subdivision is supported by the fact that the early substage,which conforms to the time period when R.praebergonii diverged from R.bergonii, have a significantly different regression coefficient as compared to the later substage (table 2); this discrepancy in direction and rate is observed in all the central equatorial sites as well as in the eastern equatorial core. Moreover, the regression coefficient before 2.7 Ma in the above sites deviates significantly from zero as opposed to after the cut-point (except 157).

Consequently, I have divided up the temporal sequence of HH into two substages; an early period (3.1-2.7 Ma) designated by a relatively rapid rate and a subsequent later phase (2.7-1.6 Ma) characterized by a relatively slower rate of change. The rate of evolution of HH in the Indian Ocean core does not suggest any major shifts that would justify the recognition of subsequences (fig. 25). Even though HH appears to remain rather constant through time it has a slope that is significantly different from zero at the 0.05 significance level (table 34).

The evolution of the width of the valve (WC) in R.praebergonii differs from AL and HH in the sense that there is no obvious shift in direction and rate of change (fig.29,38). The regression slopes for WC throughout the sampled time period (3.1-1.6 Ma) is significantly different from zero in all the central and eastern equatorial cores (table 34). To the contrary, the null hypothesis of no change was not rejected for WC in the Indian Ocean core (table 34).

In R.sigmoida the evolution of AL and WC indicates a rate slow down and a shift in the direction of change starting at 3.2 Ma in DSDP Sites 157 and 504 (fig. 16,17,35,36). However, the heterogeneity of the slopes for both AL and WC in Site 157 before and after 3.28 Ma is significant at the 5% level while this is not the case

in Site 504 (table 3,4). Consequently, the direction of evolution in AL and WC for R.sigmoida can be divided up into two substages in site 157; one characterized by a relatively rapid directional change (3.35-3.28 Ma) and the other by a rate slow down and a shift in direction (3.07-3.28 Ma). Such a subdivision in Site 504 may not be justified. The period prior to 3.2 Ma, that is when R.sigmoida diverges from R.bergonii, the rate of change in AL and WC is significantly different from zero for both sites (except WC in Site 504)(tables 3,4) while after the inflection point the slopes do not deviate significantly from zero. The temporal sequences of HH in R.sigmoida exhibit directed change which is indicated by the fact that the slopes for both sites are significantly different from zero. However, there are no major shifts in direction and rate of change as far as HH is concerned (table 34; fig. 26-27).

During the relatively short time span (3.5-1.6 Ma) R.bergonii has been incorporated into this analysis the evolution of the mean AL,HH and WC shows no apparent rate change or change in direction. Consequently these time series have not been further divided up into subsequences (fig.11,17,19,21-29). In 9 cases out of a total of 15 the regression coefficient does not deviate significantly from zero (table 34,35).

D. Patterns of morphological change

The univariate patterns of change in the mean length of the apical process (AL),the mean width of the valve (WC) and the mean height of the hyaline area (HH) were analyzed in space through simple linear regression, analysis of covariance (ANCOVA) (Zar 1984; Sokal and Rohlf 1981) using SAS GLM (SAS USER GUIDE:Statistics, version 5 1985). Where the time series of the above characters indicated a "significant bend", which was determined by visually inspecting the data, the sequence was divided and the subsections were examined separately through ANCOVA. This statistical procedure checks for the heterogeneity of regression slopes and intercepts for a particular character over a geographic region. In conjunction with multiple comparison tests (Sokal and Rohlf 1981) the ANCOVA was used in this study to approximate differences in patterns of evolution in R.praebergonii, R.sigmoida and R.bergonii separately across the investigated portion of their distribution range. Sites that occupy the same position, from a statistical point of view, on the bivariate plot, that is, they have the same regression slopes and intercepts for the variable under investigation, are here considered to exhibit the same pattern. On the other hand, dissimilarities in just the regression slopes among

localities express geographic variation in the direction of evolution while differences in just the intercept implies that the direction of change is the same.

The pattern of temporal change of the length of the apical process in the early evolutionary stage (3.1-2.7 Ma), which was artificially introduced to the Indian Ocean sequence as well as to the sequence in site 157 in order to equalize the sample sizes of R.praebergonii, appears to be different with respect to geography (table 5). Thus, the next step in the analysis is to uncover the differences in the slopes and intercepts through a multiple comparison test. In this investigation the approximate 95% comparison limits were calculated according to Gabriel by the GT2-method (Sokal and Rohlf 1981). This approach is preferred since the sample sizes are quite different (Sokal and Rohlf 1981) in the investigated cores. Those sites that have overlapping 95 % intervals for both the slopes and the intercepts estimate the same population regression. During the first stage in the evolution of R.praebergonii AL shows a homogenous pattern in the central equatorial region (RC12-66,V28-179,DSDP Site 573) while the Indian Ocean site and Site 157 form a separate group with respect to the central Pacific sites (fig.11-14,19;table 5). In site 572C, which is located in between the equatorial and the Peru water mass, the early period of the evolution of AL

is characterized by a having the same slope (direction) as the central equatorial group whereas the intercept is equal to the one found in the Indian Ocean core and in Site 157 (fig.12;Table 5). Consequently, the pattern of change is unique in the respect that it takes an intermediate position between the eastern and central equatorial patterns. The later stage (2.7 - 1.6 Ma) in the evolution of AL is characterized by two homogenous groups of patterns; one composed of the central Pacific and the Indian Ocean cores and another made up of the eastern Pacific region (Table 6). In this case Site 572C also shows a pattern similar to both groups.

The change in the height of the hyaline area for the first evolutionary stage (3.1-2.7 Ma) in R.praebergonii in the central equatorial and the Indian Ocean sites exhibits the same patterns, except core 572C, while Site 157 is unique in that respect (Table 7). In this case Site 572C also takes an intermediate position since it shows similarities in pattern of change of HH with both Site 157 and the Indian Ocean core,RC12-66 and V28-179. Based on the heterogeneity in the regression coefficients and intercepts, all the central equatorial (except RC12-66) cores as well as the Indian Ocean core indicate the same pattern of change in HH for the second evolutionary stage (2.7-1.6 Ma). However, in core RC12-66, HH shows a distinct pattern as well as in Site 157

(Table 8).

As far as WC in R.praebergonii is concerned the central equatorial sites correspond in pattern of change (table 9). In the Indian Ocean site WC does not show the same pattern of evolution as was documented in the central equatorial sites and in core 157 which is distinct with respect to the patterns of change in both the former and latter locations (table 9).

In R.bergonii AL indicates heterogenous temporal patterns with respect to geography. In this case the central and eastern equatorial (157) sites appear to change according to the same pattern (table 10). The temporal sequence of AL in the Indian Ocean and Site 504, which have distinct patterns with respect to each other, indicate heterogenous patterns in relation to RC12-66 while they show similarity to the pattern documented in 157 (table 10). As far as pattern of evolution of HH is concerned, the Indian Ocean site is distinct with regard to the other cores. However, there is no apparent difference in patterns between the localities in central and eastern equatorial Pacific (table 11). The pattern of change in WC form two separate groups, those are an eastern Pacific group and a central Pacific group which includes the Indian Ocean core. However, cores RC12-66 and 573 take an intermediate position as far as pattern of change is concerned since they are similar to both the

Indian Ocean and the eastern Pacific patterns (table 12).

As far as R.sigmoida is concerned the pattern of change in AL and WC for the first evolutionary stage (3.35 -3.1 Ma) is different in Sites 157 and 504 (fig.16-17;table 13). To the contrary, the slopes are the same which shows that the direction of change is the same in both cores but the relative position of the regression lines in bivariate space is not. For the second stage AL and WC (3.1 Ma-2.95 Ma) are similar in both locations; thus showing an identical pattern of evolution (table 13). The pattern of change in HH is distinct in each of the two sites but the direction of evolution is similar (table 13). It may be summarized that in general the results of ANCOVA indicate that all three variables in both R.praebergonii and R.bergonii tend to form distinct patterns of change with respect to the Peru water mass and the central water masses in the Pacific and Indian Ocean.

In order to address questions concerning similarities in pattern and direction of evolution as a linear relationship between the dependent variable (AL,HH, WC) during and after the morphological divergence event it is necessary to compare the regression coefficients and intercepts for heterogeneity. If both lineages, that is ancestor and descendant, estimate the same regression, that is the slopes and the intercepts

are similar, a divergence event cannot be recognized, at least from a statistical point of view.

During the first (3.1-2.7 Ma) as well as the second stage (2.7-1.7 Ma) in the evolution of R.praebergonii from R.bergonii AL appear to exhibit distinct patterns and direction of change; this is evidenced by significantly different intercepts and slopes for both phases in cores RC12-66, 573, as well as for site 157 and the Indian Ocean core (fig.13-15,19;table 14). The same results are also obtained for the recognized substages for HH as well as for WC but with two exceptions (fig.22-25,30,32,34,38;tables 15,16). The null hypothesis of equality of the slopes for the second evolutionary stage of HH and the whole sequence of WC in Site 573 was not rejected by the F-test ($P>0.05$) even though the intercepts were dissimilar; this implies that the direction of change is the same but not the pattern (table 15).

The divergence of R.sigmoida from R.bergonii in Site 157 as indicated by AL, HH and WC (fig.16,26,36), is also supported by the comparison of the regression intercepts and slopes for the recognized substages in that these are significantly different and thus the direction and pattern of change is distinct in both lineages (table 17-19). However, the exception to this is found in the second evolutionary stage (3.1-3.0 Ma) of WC

where the slopes for both R.sigmoida and R.bergonii is the same (P>0.05) but the intercepts are different. Consequently, the direction of change is similar but the patterns are unique for both lineages since the intercepts are significantly different (P<0.05). This also characterizes the morphological divergence and subsequent change for the recognized substages of AL,HH and WC in core 504 (table 17-19;fig. 17,27,35).

In summary: The overall result shows that during and after the morphological divergence event both AL and HH are characterized by distinct patterns as well as direction of change in R.praebergonii and R.bergonii. Even though divergence in WC is not as apparent as in the other variables the analysis suggest that R.praebergonii and R.bergonii have distinct patterns for this character, as well. The results of the analysis make the divergence of R.sigmoida from R.bergonii, as evinced from the figures 17,27 and 35, hard to interpret since in Site 157 the patterns appear distinct with respect to each lineage but that is not the case in core 504.

E. Hierarchical linear models

Bookstein et al. (1978) proposed a methodology for analyzing temporally ordered data from the fossil record for punctuated equilibrium, phyletic gradualism and

stasis by estimating the comparative contribution of each model to explaining the variance in the raw data. This is done by fitting a set of hierarchical linear models to the data through linear regression techniques (see appendix C for instructions to the models). The method is hierarchical in the sense that the total variance explained by the most general (most inclusive) model in its class, that is the one having the largest number of parameters, can be further explained by more specialized (simpler) models with a lower number of parameters. A "step-down F-test" (see appendix I in Bookstein et al. 1978;Zar 1984) is used to choose the best-fitting model, that is to find the simplest model in the hierarchy which is not significantly different from the most inclusive model in terms of explaining the variance in the data (Bookstein et al 1978).

In my work I have used this idea for "building" linear representations of evolution; thus I have both used and extended Bookstein et al's (1978) original linear models as well as generated a new set of hierarchical linear models for testing the morphological divergence events for punctuations, phyletic gradualism and stasis in the investigated characters (fig. 39-41). These linear representations were constructed with the intention to quantify the morphological evolution not only during and prior to the divergence of the descendant

from its ancestor but also after the time the descendant has become an established morphotype, which is inferred from an apparent "node" in the data. Such a class of models is of great interest in testing the relative frequency of the weak and the strong version of punctuated character stasis in the data (terminology adopted from Hecht and Hoffman 1986). The former is consistent with gradual phyletic change taking place at varying rates while the latter rejects the idea of phyletic character gradualism and the weak version of punctuated character stasis. Moreover, I have also used and extended some of Bookstein et al's (1978) single "species" models to comprise a "node" where the direction of evolution changes. Thus, the following hierarchical linear models (illustrated in fig. 39-41) have been fitted to the data in this study using the REG procedure in SAS (SAS USER GUIDE:Statistics, version 5 1985):

I. One lineage without "break".

   1. character gradualism in one lineage.

II. One lineage and one "break".

   2. Stage 1: character gradualism; Stage 2: character stasis.
   3. Stage 1: character stasis; Stage 2: character gradualism.
   4. Stage 1: character gradualism; Stage 2: character gradualism.

III.Two lineages and one "break".

5. Character stasis in lineages 1 and 2; lineage 2 originated from lineage 1 through a character punctuation.
6. Character stasis in lineage 1 and character gradualism in lineage 2; lineage 2 originated from lineage 1 through character gradualism.
7. Character gradualism in lineage 1 and character stasis in lineage 2;lineage 2 originated from lineage 1 by remaining in character statis while lineage 1 changed gradually in the character.
8. Character gradualism in lineages 1 and 2; lineage 2 originated from lineage 1 through character gradualism while lineage 1 changed gradually in the character.
9. Character gradualism in lineage 2 and character stasis in lineage 1;lineage 2 originated from lineage 1 by a character punctuation after which it continued to change gradually in the character.
10. Character gradualism in lineage 1 and character stasis in lineage 2; lineage 2 originated from lineage 1 through a character punctuation after which it remained in character stasis.
11. Character gradualism in lineages 1 and 2; lineage 2 originated from lineage 1 through a

character punctuation after which both lineages continued to change gradually in the character.

IV. Two lineages and two "breaks".

12. Character stasis in lineage 1 and character gradualism (b) and subsequent character stasis (a) in lineage 2; lineage 2 originated from lineage 1 through character gradualism.
13. Character stasis in lineage 1 and character gradualism (b) and subsequent character stasis (a) in lineage 2; lineage 2 originated from lineage 1 through a character punctuation.
14. Character gradualism in lineage 1 and character gradualism (b) and subsequent character stasis (a) in lineage 2; lineage 2 originated from lineage 1 through character gradualism after which lineage 1 remained in character stasis while lineage 2 changed gradually.
15. Character stasis in lineage 1 and successive character gradualism (a,b) in lineage 2; lineage 2 originated from lineage 1 through character gradualism.
16. Character stasis in lineage 1 and successive character gradualism (a,b) in lineage 2; lineage 2 originated from lineage 1 through a character punctuation.
17. Character gradualism in lineage 1 and character

gradualism (b) and subsequent character stasis (a) in lineage 2; lineage 2 originated from lineage 1 through character punctuation.

18. Character gradualism in lineage 1 and successive character gradualism in different directions (a,b) in lineage 2; lineage 2 originated from lineage 1 through character gradualism.
19. Character gradualism in lineage 1 and successive character gradualism (a,b) in lineage 2;lineage 2 originated from lineage 1 through a character punctuation.

The hierarchical linear models were fitted through piecewise linear regression with the three lineages, R.praebergonii,R.sigmoida and R.bergonii defined apriori, to the temporal scatter of each of the three variables separately. The category of models fitted were determined by the presence of a "break" between the ancestral and descendant lineages and "nodes" or a shift in the direction of change within either the former or latter. The model that best represent the pattern of evolution was determined by a "step-down F-test" (parsimony criterion).

The initial "break" at 3.1 Ma between R.praebergonii and R.bergonii for all three variables took place through a significant punctuation as opposed

to gradual change in 10 out of 12 possible cases (tables 23-24; fig. 58,59,61,63, 53,55,56,42,44,45). Likewise, as R.sigmoida branched off from R.bergonii at 3.2 Ma, a significant punctuation in all three traits appears to have dominated the event since in only 1 case out of 6 gradual change took place (tables 23-24; fig.48,49,50,51,60,62). In both R.praebergonii and R.sigmoida AL,HH and WC continued to evolve in a gradual manner after the incipient first appearance, except after the first appearance of R.praebergonii in the Indian Ocean where AL remained static (table 23; fig.58,53,42). As R.praebergonii and R.sigmoida became established as distinct lineages (2.7 Ma and 3.1 Ma) the former remained static as opposed to showing gradual change for all three characters in 7 cases out of 18 (includes the cores where just R.praebergonii was sampled) while the latter showed stasis in the AL,HH and the WC in 2 cases out of 6 (tables 23-24; fig.42-65). R.bergonii exhibited character stasis 11 times out of a possible 15, that is gradual change appears to have been infrequent. The best fitting linear representation of the evolution of AL and HH in all three lineages accounts for between 0.65 to 0.80 of the sum-of-squares while WC indicates a much lower range, that is between 0.06 to 0.61 (tables 23-24).

F. Random walk

In studies of tempo and mode in morphological evolution the appropriate null hypothesis is a random walk since it is the "simplest" explanation for a temporal sequence of mean values (Bookstein 1987 and pers.commun.). Consequently, this null hypothesis should be tested and if it is not rejected the results are very difficult to interpret. This is because failure to reject the null model does not necessarily imply random morphological change in a population. In fact, shifts in the relative frequencies of morphotypes in a population may very well be deterministic since the causal factor(s) may vary randomly. However, if the null model is rejected stasis and anagenesis are deviations from the central random walk model in "opposite directions" (Bookstein 1987). Bookstein (1987) has developed a statistic from the mathematical literature of random walk which can be applied to empirical data, such as mine. Consequently, this Range Test will be used to investigate the presence of temporal random walks in the mean values of AL,HH and WC of the three Rhizosolenia forms. The "reduced speeds" (eq.1) form the basis for calculating the test statistic x. According to Bookstein (1987) the reduced speeds (ratio), which is the expected deviation from starting size (microns) under a random walk in the examined character over a fixed time interval of one million

years, is calculated based on the following equation:

$$\frac{|S_{nk} - S_{nk-1}|}{(n_k - n_{k-1})^{0.5}} \qquad \text{(eq.1)}$$

$|S_{nk} - S_{nk-1}|$ is the absolute difference in morphology between two subsamples which is scaled by the square-root of the elapsed time, or $(n_k - n_{k-1})^{0.5}$, between the two subsamples.

The upper 5% of the distribution of x, that is values above 2.25, is in this study considered to represent change improbably large (probability of leaving the range expected under a random walk) for being due to a random walk alone; consequently an evolutionary interpretation of anagenesis. Likewise, the lowest 5% of the distribution of the test statistic x or 0.62 represents temporal variation which is improbably constrained (probability of leaving the range expected under a random walk), thus corresponding to stasis. The null model of random walk separates these two findings by an interval incorporating values between 2.25 and 0.62. The procedures for calculating the test statistic x and the corresponding probabilities are taken from Bookstein (1987).

In every one of the three investigated regions, those are the Indian Ocean core, core RC12-66 in the central Pacific Ocean and DSDP Site 157 in the eastern Pacific Ocean, AL in R.praebergonii was found to have x-

values ranging from 2.49 to 5.227 with corresponding probabilities between 0.976 and 0.99999 of leaving the range expected under a random walk (table 20). Hence, the pattern of evolution in AL in these sites can be interpreted as being anagenetic (fig.74,76,77; table 20). To the contrary, the apparent changes in the length of the apical process of R.praebergonii in cores V28-179, 573 and 572C of the central Pacific Ocean were all consistent with a random walk (fig.78,74,73;table 20). The temporal sequence of mean HH in R.praebergonii in the Indian Ocean core, core RC12-66, Site 573 and Site 157 are all consistent with anagenesis (table 21; fig.80,81,83,84). For instance, in RC12-66 the x=4.089 which corresponds to a probability 0.9999 of leaving the range expected under a random walk; this is strongly suggestive of anagenesis. The time-series of HH in V28-179 and Site 572C conform to the null hypothesis (table 21;fig. 79,82). As far as WC is concerned, cores RC12-66,V28-179,573 and 157 indicate temporal variability which is quite typical of a random walk (table 22; fig. 92,94,96,97). Nevertheless, two temporal sequences - one in Site 572C and the other in the Indian Ocean core - show significant anagenetic change in WC (table 22;fig.93).

The evolution of AL in R.bergonii is compatible with anagenesis in core RC12-66 and Site 157 (table 20;

fig.66,69). However, this is not the case in the Indian Ocean core,Site 573 and Site 504 where the x values are 1.4186, 2.1299 and 1.0009 respectively with corresponding probabilities of 0.695, 0.93 and 0.37 of leaving the range expected under a random walk (table 20;fig.67,72). Moreover, in all the sites where R.bergonii was sampled the time series of HH was found to be incompatible with random walks (table 21;fig. 87,88,89,90,91). For instance, the change of HH in Site 157 and core RC12-66 tend very strongly against anagenesis, as evidenced by two improbably high x-values, 3.556 and 3.283 respectively, (table 21;fig. 87,91). In the other two sites, that is the Indian Ocean core and Site 504, the variable is found to be significantly in stasis (table 21;fig. 88-89). WC of R.bergonii in the Indian Ocean core as well as in the core RC12-66 and Site 504 follow a random walk through time (table 22;fig. 104,103,101). However, in Sites 157 and 573 the temporal sequence of WC are significantly in anagenesis (table 22;fig. 100,102).

As far as R.sigmoida is concerned the time series of AL,HH and WC in both Sites 157 and 504 are all in agreement with a random walk (tables 20-22;fig.70-71,85-86,98-99).

In summary: the temporal variation in AL and HH in R.praebergonii,R.bergonii and R.sigmoida exhibit anagenesis in 11 cases,stasis in 2 cases and random walks

in 13 situations out of a total of 26. Most of the nonrandom variation is concentrated around the length of the of the apical process and the height of the hyaline area of R.praebergonii and R.bergonii. WC of the three lineages is significantly in anagenesis in only 4 cases and it vary randomly 9 times out of a total 13.

G. Geographic/ecophenotypic variation

Since the presence of geographic variation in conjunction with directional migration could obscure local patterns of temporal change in morphology I have analyzed the spatial variation in AL,HH and WC of R.praebergonii and R.bergonii at approximately synchronous time levels through Tukey's studentized range test (multiple comparison test) (Zar 1984) using SAS GLM (SAS USER GUIDE:Statistics). This approach may lead to important conclusions about population distribution patterns. Such spatial heterogeneity in the investigated variables may have a genetic or nongenetic basis which will be discussed later on in this paper.

During the first evolutionary stage (3.1-2.7 Ma) of R.praebergonii, Tukey's studentized range test for the length of the apical process indicate two distinct groupings at the 0.05 significance level. One is composed of the central Pacific cores (RC12-66,V28-179,573) and the other is constituted by the eastern Pacific core and

Site 572C (table 25). At the time of the first appearance (2.91 Ma) of R.praebergonii in the Indian Ocean AL shows greater resemblance to the same variable in Sites 157 and 572C than to the central Pacific cores while at 2.7 Ma this situation is reversed (table 25).

The height of the hyaline area in R.praebergonii shows a rather similar spatial pattern for the same time period, that is 3.1-2.7 Ma, in the sense that cores 157 and 572C tend to form a homogenous cluster (table 27). However, in this case HH in 572C also shows some affinity to the same trait in the rest of the sites (table 27). On the other hand, HH of R.praebergonii in the Indian Ocean site blends rather well with the same form in the central Pacific locations. In addition, HH in core 573 have a tendency to form a distinct group with respect to cores RC12-66 and V28-179 as well as to Sites 157 and 572C (table 27).

Even though WC of R.praebergonii is not divided into substages, I will still present the results of the Tukey test for this variable throughout the same time period. Contrary to the findings for AL and HH, WC does not indicate any specific pattern of geographic variation from 3.1 Ma to 2.7 Ma. (table 29). There might be a slight tendency for WC in R.praebergonii in Sites 572C and 157 to group together but this is far from being as obvious as it is for AL.

During the time period after 2.7 Ma, that is when R.praebergonii became established as a separate lineage, the spatial variation in AL is characterized by core 157 forming a distinctive homogenous group as compared to the central Pacific and Indian Ocean cores (tables 25,26). With some exceptions, AL in the Indian Ocean core and Site 572C show a much stronger resemblance to the central Pacific cores (RC12-66,V28-179 and 573) throughout the second substage (2.7-1.7 Ma) of the morphological change in R.praebergonii than during the first stage (3.1 - 2.7 Ma) (table 25,26). Generally, sites RC12-66,V28-179,573 and 572C form a homogenous cluster as far as the mean length of the apical process is concerned. However, the sampling of R.praebergonii after the Matuyama/Gauss boundary (2.46 Ma) in V28-179 was not continued and is therefore not included in the analysis after this event. In Site 572C R.praebergonii was not sampled past 2.04 Ma because the sediments in this core has not been correlated to a paleomagnetic reversal record past that time.

Contrary to the rather specific pattern of geographic variation characterizing the early stage in the evolution of HH the spatial diversity of the same variable for the time period after 2.7 Ma lacks overall orderliness in R.praebergonii (tables 27,28). Nevertheless, the eastern equatorial site tend to be a

distinct geographic group, especially from 2.6-2.3 Ma even though it is not as clear as for the time before 2.7 Ma. Moreover, the central Pacific and the Indian Ocean cores appear to be a less homogenous group as compared to the early stage (tables 27,28).

As opposed to the early phase of WC, there seems to be more of a pattern to the geographic variability of this character in R.praebergonii after the inflection point at 2.7 Ma since the Tukey test indicates that Site 157 tends to form a separate group in relation to the other cores (tables 29,30). Consequently, the central Pacific sites are also a more homogenous assemblage (RC12-66,V28-179, 573 and 572C) while WC of the Indian Ocean core show affinity to both the eastern and the central Pacific aggregations at different time levels; thus showing instability (tables 29,30).

Based on the analysis of the geographic variation in the length of the apical process in R.bergonii in the locations where it was sampled, the most obvious pattern is that the central Pacific cores (RC12-66 and 573) form a group different from the eastern Pacific (table 31). However, AL in 157 indicates some similarity with the central cores, particularly with Site 573, but otherwise it tend to show resemblance to core 504. On the other hand, the AL in the Indian Ocean site conforms to the central Pacific assemblage but never with the eastern

Pacific cores. These results are in concordance with the findings for the spatial variation of AL in R.praebergonii during the second phase of morphological change (2.7 - 1.7 Ma).

To the contrary, HH of R.bergonii seems to be quite unique in the Indian Ocean site at the compared time levels since the Tukey's multiple comparison test group core RC12-66 and Site 573 with Sites 157 and 504 more often than with the Indian Ocean core (table 34). Consequently, the central and eastern Pacific cores form the second cluster which is not as homogenous internally. The lack of a spatial pattern appears to be characteristic of HH in R.bergonii in the Pacific Ocean which also was the case with the same variable of R.praebergonii during the later phase of evolution (2.7 - 1.7 Ma).

There is a much lower tendency of WC in R.bergonii to separate itself into distinct geographic groups at the investigated temporal horizons. Nevertheless, when the WC form spatial aggregates the central cores generally are more similar to each other than they are to the eastern and the Indian Ocean sites which also tend to form a homogenous group (table 33).

The among location differences in mean AL, HH and WC in R.sigmoida was examined on synchronous time levels through a T-Test (SAS USER GUIDE:Statistics). Based on

this analysis WC shows no differences in mean morphology between Sites 157 and 504 while HH indicates an inconsistent pattern. AL appears to distinct in both locations as far as mean morphology is concerned.

In summary it may be concluded that there is a general tendency for all three characters in R.praebergonii and R.bergonii to form homogenous cluster with respect to the central equatorial and the Peru water mass.

XII. DISCUSSION

A. Modes of lineage origination

Based on the ancestral-descendant analysis of the investigated characters I conclude that R.praebergonii and R.sigmoida evolved from R.bergonii through a branching event in the equatorial Pacific Ocean. There are several different models of lineage origination, such as allopatry,sympatry and parapatry (e.g. Mayr 1963; Bush 1975; Endler 1977), which have been shown to be applicable for interpreting morphological divergence among planktonic microfossils, including diatoms (reviewed by Lazarus 1983). Since all of the above models may give rise to branching patterns of lineages in the fossil record I will evaluate the compatibility of the predictions of each of these theoretical models with the

data obtained in this work.

Mayr's (1963,1979) peripheral isolate model, which essentially states that new lineages originate in small isolated populations through a "genetic revolution",is closely associated with the prediction of punctuation and stasis in the paleontological record. Thus, no intermediate morphologies would be expected if R.praebergonii and R.sigmoida originated from R.bergonii in a peripheral isolate and subsequently became sympatric with their ancestor; this is because the likelihood of recovering such intermediate types as well as isolates in the fossil record is remote. In fact, there exist many transitional forms between the ancestor and the descendant in all the Pacific Ocean cores; this would argue against an allopatric origination in small separated populations. However, this is not the case in the Indian Ocean core where R.praebergonii appears to have arisen from R.bergonii through a punctuation. This morphological gap may be due to directional migration of the R.praebergonii from its site of origination in the Pacific Ocean or to independent origination in conjunction with parallel evolution (fig. 9-10). In addition, small, isolated environments may not exist for fully oceanic plankton forms, such as those studied in this work, since the distribution and structure of these populations generally coincide with the major water

masses and current systems (Lazarus 1983). These bodies of water are known to be well mixed on a global scale over approximately a 1000 year period (Lazarus 1983 and references therein). Based on the above arguments the peripheral isolate model of Mayr (1963,1979) is a very unlikely explanation of the morphological divergence of R.praebergonii and R.sigmoida from R.bergonii in the Pacific Ocean. In general, this model may not be the primary mode of origination of new lineages among pelagic protists (Lazarus 1983).

Another alternative for explaining the observed morphological divergence events in the three Rhizosolenia lineages is equal allopatry or geographic isolation of large populations through extrinsic barriers. This takes place through an initial subdivision of a large,geographically widespread species into approximately equally large populations after which there is gradual divergence in morphology between the two isolated groups. This model has also been advocated by Mayr (1963, 1979) and referred to by Eldredge and Gould (1972) as the basis for phyletic gradualism. Consequently, one would expect to find two initially similar morphologies diverge gradually in two isolated areas till they reach the status of different species. If the barrier break down the ancestral and descendant forms would possibly show character displacement if they are

"too similar" after they have become sympatric (e.g. Kellogg 1983,1976). In the neosympatric phase intermediate morphologies would most likely be absent but this depends on the degree of separation between the ancestor and descendant when they meet again. Lazarus (1983) has pointed out that possible isolating mechanisms in the oceanic holoplankton would be continental barriers and bipolarity. As far as the branching of the Rhizosolenia lineages is concerned the equal allopatry model cannot be used to explain this phenomenon primarily because there are no "stable" barriers, such as land masses, which could have barred the descendant from the ancestor. Had,in fact, this pattern of morphological change been the result of allopatric speciation, for instance in the Atlantic Ocean, and subsequent neosympatry in the Pacific Ocean the transitional forms of R.praebergonii and R.sigmoida would most likely not have been encountered in this study. In addition, since R.praebergonii appeared 200.000 years later in the Indian Ocean as compared to the Pacific Ocean, the absence of intermediate morphologies in the Indian Ocean is probably not a result of subsequent reestablishment of neosympatry but most likely due to primary directional migration during its origination in the Pacific Ocean. If migration was the case it probably took place in conjunction with morphological change. An alternative explanation would be

that R.praebergonii may have originated independently from R.bergonii in the Indian Ocean after which it went through parallel evolution. This is supported by the fact that R.praebergonii appeared earlier in the Indian Ocean as a distinct morphotype in relation to the Pacific Ocean. However, R.praebergonii appeared earlier in the latter place but as a transitional form. Based on these arguments, equal allopatry is also a rather unlikely explanation for the origination of R.praebergonii and R.sigmoida at least in the Pacific Ocean.

However, diversification of morphology along an environmental gradient has been recognized by Lazarus (1983 and references therein) as an important mode of evolution in the oceanic holoplankton. Endler (1977) has described in detail, the parapatric model of speciation or how clinal variation in morphology may give rise to new lineages even in absence of barriers to gene flow. Since origination of a new lineage along a geographic trend in morphology of the ancestor in the pelagic realm involves large populations it is most likely a gradual process and in many cases isolation by distance is of primary importance (Lazarus 1983). However, the parapatric model may in some cases be hard to distinguish from the allopatric model and subsequent contact since a stepped cline in the transition zone between ancestor and descendant looks like a branching event through time. For

instance the divergence of the radiolarian Eucyrtidium matuyami from E.calvertense was interpreted by Hays (1970) and Kellogg (1976,1983) as an example of an allopatric speciation event while Lazarus (1983) argues that it might very well be the origination of a new lineage by the parapatric model since the presumed oceanographic barriers didn't prevent gene flow.

The parapatric model makes some specific predictions about the morphological patterns which can be investigated in the microfossil record. Firstly there has to be a significant latitudinal or longitudinal trend in the presumed ancestral form; secondly the stepped cline, which should look like a divergence event where the ancestor and descendants overlap in their distribution, should form gradually in a specific region, possibly associated with a weak oceanographic barrier; thirdly the descendant or the ancestor should either be absent from one end of the cline or if present there should exist a morphological gap between the two lineages unless they have converged in their morphology. None of the expected patterns can be discerned in this study. Most importantly the presumed ancestral form, R.bergonii, does not indicate a longitudinal trend prior to the first appearance of R.praebergonii and R.sigmoida. In addition, the most obvious transition from R.bergonii to R.praebergonii takes place throughout the Pacific Ocean

and not in a restricted region. Both ancestor and the descendants are found at each end of the investigated distribution range after the branching event. Only in the Indian Ocean an obvious "gap" exist between R.bergonii and R.praebergonii which is thought to be a result of primary directional migration in conjunction with morphological change or possibly independent origination followed by parallel evolution. Questions have also been raised by Lazarus (1983) about the importance of morphological variation along a depth gradient for evolution among radiolarians. This probably does not apply to the planktonic diatoms in this study since the surface water is well mixed over a short periods of time (weeks) which would prevent total stratification and thus prevent clines from forming isolates.

Either a sympatric branching event in a restricted area somewhere in the Pacific followed by geologically rapid dispersal (cf. Buzas and Culver 1986) or a morphological branching event, which took place at the same time, throughout the distribution ranges in the Pacific Ocean, seems to be the most likely mode of origination of R.praebergonii and R.sigmoida. However, the available resolution is not fine enough to distinguish between these possibilities. The presence of a substantial number of intermediate forms of R.praebergonii and R.sigmoida that slowly diverged from

R.bergonii throughout the respective distribution range in the Pacific Ocean as well as the temporal coexistence of the ancestor and descendant until the latter disappeared in all the investigated sites lend strong support for the sympatric model as opposed to the unequal allopatric model (fig. 16-17,35-36). This model is further substantiated by the fact that these diatom lineages must have lived in the well mixed photic zone of the oceanic realm due to their photosynthetic activity. Consequently, they probably could not have differentiated into separate depth habitats or along a depth gradient. In the Indian Ocean the transitional forms between R.bergonii and R.praebergonii are absent which is also expected since the latter most likely did not evolve there but instead arrived there as an immigrant. This is supported by the fact that R.praebergonii appeared in Indian Ocean 200,000 years later or at approximately 2.9 Ma. Such a step-wise pattern of first appearances indicates that R.praebergonii migrated into the Indian rather than originated there. However, if R.praebergonii originated independently in the Indian Ocean it must have undergone parallel evolution; this is primarily supported by the fact that R.praebergonii appeared as a distinct morphotype earlier in the Indian than in the Pacific Ocean. The 200.000 year time discrepancy between the first appearance of R.praebergonii in the Indian and the

Pacific Ocean could be a result of a sea-level fall during Pliocene-Pleistocene glaciations (Shackleton and Opdyke 1977). Such an event would have interfered with the water flow from the Pacific to the Indian Ocean thus delaying a population build up of R.praebergonii in the Indian Ocean (Potts pers.comm.). Potts (1984) also suggests that the sea level could have been as much as 130 m lower than the present one at 3.2 Ma, thus increasing the size of the continental shelf along the Central Indo-Pacific coastline.

It can be concluded that R.praebergonii and R.sigmoida diverged from R.bergonii most likely through a sympatric event in the Pacific Ocean after which the former migrated out from there. An alternative explanation may be that R.praebergonii originated independently in the Indian Ocean after which it underwent parallel evolution.

B. Environmental factors and morphological change

Since the morphological divergence of R.praebergonii and R.sigmoida from R.bergonii presumably took place in the homogeneously mixed surface water masses of the Pacific Ocean there must have been biotic and/or abiotic factors involved, unless the event was totally random; the latter possibility will be dealt with later on. There is a good oxygen isotope record available

in Site 572C as well as in other sites, which may indicate for instance temperature changes in the surface waters and shifts in ice volume; this information can be compared to temporal change in morphology.

According to Prell (1985) there is a positive shift in the planktonic oxygen isotope ratio ($^{18}O/^{16}O$ ratio) in Site 572C at 44 meters or at about 2.9 Ma. Similar patterns are also apparent in the benthic ^{18}O record of North Atlantic Hole 552A (Shackleton et al 1984) as well as in other low-latitude planktonic data (Prell 1984). Since there is similar variability in the planktonic and the benthic record the isotope event indicates ice volume changes at 2.9 Ma. (Prell 1985). On the other hand, a geographically widespread positive shift in the oxygen isotope ratios of benthic formaminifers, which is not observed by Prell in 572c or in any other low latitude cores, has been dated at 3.2 m.y. (e.g. Shackleton and Opdyke 1977; Hodell et al 1985) and at 3.4 m.y.(Kennett 1986;Elmstrom and Kennett 1986). Prell (1985) has offered a possible explanation for the discrepancy between the findings of the benthic and the planktonic record as follows: that benthic data records an increase in ice-volume at 3.2 Ma whereas the planktonic data indicate a warming of the surface water or decrease in salinity. An alternative idea, also offered by Prell (1985), is that no permanent addition of ice volume was initiated at 3.2

Ma but instead a short term increase in ice volume may have occurred provided that the benthic record is sensing a cooling of bottom water temperatures at 3.2 Ma from high latitudes. The second explanation Prell (1985) considers as the more plausible one. Besides the transition in isotopic values at 44 meters, Prell (1985) also sees a strong maximum event at about 2.4 - 2.5 Ma in Site 572C; this has been widely noted in the literature and interpreted as an indication of the onset of northern hemisphere glaciation (e.g Shackleton et al 1984).

Noteworthy is the fact that the 2.9 Ma change of the ^{18}O record occurred within approximately 0.3 m.y. of the level at which the R.praebergonii originated from R.bergonii and that the 3.2 Ma event, which was observed for instance in core V28-179 (Shackleton and Opdyke 1977), took place as R.sigmoida developed in the eastern equatorial Pacific Ocean. These abiotic factors may have played a role in the initiation of the evolution of the lineages. For instance, Cronin (1984) found a strong correlation between unidirectional sustained climatic change and speciation events taking place within the marine ostracode genus Puriana in the middle Pliocene (4-3 Ma) as well as a relationship between character stasis and short term oscillations in abiotic parameters. Similarly, taxonomic diversification in Neogene planktonic foraminifera is thought to have been driven by

an increase in polar to equatorial thermal gradients and related subdivision of surface water masses (Wei et al 1986). Malmgren and Berggren (1987) also found a close agreement in timing of evolutionary and paleoceanographic change in planktonic foraminifera during late Neogene. Thus there may be a connection between abiotic environmental perturbations and morphological change at least in some marine microfossils. Such a relationship is predicted by the stationary model of Stenseth and Maynard Smith (1984), but can also be accommodated by van Valen's (1973) Red Queen hypothesis. The possibility that abiotic environmental factors may play a role in triggering morphological change requires further investigation.

A possible biotic factor that may have been involved in the morphological divergence of R.praebergonii and R.sigmoida is interspecific and intraspecific competition in a nutrient-limited environment. Under such conditions cell size tends to decrease since small-celled species tend to have low K_s values (nutrient concentration supporting one-half of the maximum uptake rate) and thus be more competitive in terms of nutrient uptake (Kitchell 1983). Both R.praebergonii and R.sigmoida appear to have undergone a general size decrease in relation to R.bergonii since the traits measured became smaller during the branching event. One plausible explanation out of many for the

origination of R.praebergonii and R.sigmoida from R.bergonii is that interspecific competition restricted the resources used by the ancestral population, which also intensified intraspecific competition, resulting in specialization or "fragmentation" within the R.bergonii population on the available resources. In other words there were two "solutions" to the same problem (two adaptive peaks) leading to dimorphism which consequently alleviated the intraspecific competition generated by interspecific competition.

The other important biotic interaction is "grazing" (predation) in which potential "prey" species experience differential rates of mortality dependent on predatory preference; this must represent an important evolutionary force. Marine copepods are presently the dominant predators of phytoplankton (Conover 1978). In fact, there is a tremendous amount of literature which has documented selective discrimination by copepods with respect to phytoplankton size classes even though the mode of selection remains controversial (Kitchell 1983 and references therein). If copepod grazing is selective, then particular morphological and behavioral traits that reduce the intensity of predation will be favored. For instance, marine planktonic diatoms, which are incapable of active escape, exhibit antipredatory adaptations such as spiny projections, colony formation as well as

giantism and dwarfism (Kitchell 1983 and references therein). A study by Richman et al. (1977) demonstrated high selectivity to phytoplankton sizes corresponding to peak densities but negative selectivity for sizes of phytoplankton between density peaks. Moreover, Cowles (1979) found that diet breadth of three copepod species declined as phytoplankton prey became increasingly abundant.

In this case it is not possible to determine the relative importance of abiotic and the biotic factors or the possible interactions between them in triggering the morphological divergence events.

C. Random walk

The results of the Range Test are very difficult to interpret since the failure to reject the null hypothesis of a random walk does not necessarily imply random morphological change in a population; this has for instance been pointed out by Fisher (1986). In fact, shifts in the relative frequencies of morphotypes in a population may very well be deterministic even though the test statistic indicates a random walk since the causal factor(s), which are tracked by the deme, may vary randomly. Moreover, another important aspect of this study, which make the results of the Range Test hard to interpret when the null model has been rejected, is that

the morphological branching event between R.praebergonii and R.bergonii is found to take place both in the central and eastern equatorial Pacific at about the same time. Since the Peru and the central equatorial water mass supposedly represented two semi-isolated or not fully panmictic populations of the above lineages (evidence for this will be discussed later) it can be presumed that the branching event is a result of some common cause rather than randomly diverging morphologies.

The mean length of the apical process indicates an anagenetic pattern of change in R.praebergonii in the Indian Ocean core,core RC12-66 and Site 157 while the same time-series is random in cores V28-179, 573 and 572C (table 20). How should these discrepancies be interpreted? Based on the Range Test, AL. shows a trend in RC12-66 since the x-value is well past the 0.9999 tail of its distribution (table 20). Since Sites V28-179 and 573 are located relatively close to RC12-66 as well as in the same water mass R.praebergonii in these cores must have been part of the same panmictic population in the central equatorial region and accordingly it should have evolved in a similar fashion; this is also indicated by the ANCOVA (discussed later). This interpretation also applies to R.praebergonii in Site 572C which could have been affected by migration of unique morphotypes from the partially isolated population in the eastern equatorial

Pacific, thus giving rise to a spuriously random temporal sequence of AL. On the other hand, the discordance between the findings in cores RC12-66 and V28-179 can be explained by the fact that the Range Test applied to such short sequences (500,000 years) does not "behave" (Bookstein,pers.comm.). The other two sites, those are Sites 573 and 572C, probably give rise to deviating results with respect to RC12-66 possibly due to sampling error and local differences in preservation. Consequently, the pattern of evolution in all the central equatorial sites should be interpreted to follow the same anagenetic pattern that is observed in RC12-66. The hypothesis of the trend of AL in R.praebergonii being due to some common environmental cause is further supported by the fact that the eastern equatorial population also indicates anagenesis at about the same time as in the central Pacific population.

Anagenesis was also found to dominate the pattern of change of HH in R.praebergonii in the Indian Ocean core as well as in RC12-66,573 and 157 (table 21). For this trait the null hypothesis of a random walk was also rejected in site 573 in addition to RC12-66 which in this case also exhibits a x-value which reaches past the 0.9999 tail of the distribution of this statistic. Such high probability of leaving the range expected under a random walk is very likely to be an indication of a

directional pattern of evolution. The change of HH in R.praebergonii in Site V28-179 can also be disregarded due to the relatively shortness of this sequence while the results in Site 572C may be given the same interpretation as for AL,that is "false" randomness due to migration of unique morphotypes from the eastern population. In this case the eastern equatorial population also exhibit highly significant anagenesis in HH at the same time it took place in central Pacific population which gains further support for this trend being a reaction to some common environmental factor(s).

R.praebergonii in the Indian Ocean region may also be considered to be a semi-isolated population with respect to the central Pacific deme. Consequently, the directional evolution of AL and HH of R.praebergonii in the Indian Ocean as well as in the Pacific Ocean well after its origination also lends further support for a widely spread environmental factor being involved. However, the first appearance of R.praebergonii in the Indian Ocean, which may be a result of directional migration (see later discussion), cannot be considered to be simultaneous with the same event in the central and eastern equatorial Pacific.

The change in the mean width of the valve in R.praebergonii is consistent with a random walk in the eastern and central equatorial cores, except Site 572C

(table 22). This core has a very unique position in the Pacific Ocean in that it was drilled in an area where the central equatorial and the Peru water masses meet. Thus the evolutionary patterns in this site could have been affected by environmental parameters unique to each location as well as migration of distinct morphotypes between the eastern and central region (geographic variation will be discussed later). In the latter case the temporal pattern of change could be confounded giving rise to a spurious anagenetic pattern of change in WC of R.praebergonii. The temporal sequences of AL and HH in R.praebergonii in Site 572C also deviated from the findings in the more centrally located cores as well as the sampled location (157) in the east. Although WC in Sites RC12-66,V28-179,573 varied through time in a random fashion it cannot be determined whether this is due to a deterministic tracking of a randomly varying causal factor(s) or not. A more likely explanation is that developmental constraints (Hecht pers.comm.) and selection operated on this character at the extremes of an adaptive peak within which WC was free to vary randomly (cf. Raup and Crick 1981). The same explanation can also be applied to the sequence in Site 157. The width of the valve exhibited a significant increase in the Indian Ocean after R.praebergonii arrived there which may be a consequence of the uniqueness of the

environment.

All three variables of R.sigmoida in both Site 504 and 157 are consistent with a random walk (tables 20-22) which is not an unexpected outcome of the Range Test because it is rather ineffective for detecting stasis or anagenesis for such short temporal sequences (~0.3 m.y.) (Bookstein pers.comm.). However, the branching events between R.sigmoida and R.bergonii were recovered in both sites within the same population which indicates that the observed morphological divergence was probably not due to sampling error. Moreover, due to the large size of phytoplankton populations drift is unlikely to have taken place. Based on the iterative pattern of evolution of AL, HH and WC with regard to R.sigmoida and R.praebergonii in 157 it appears as if an "ecological opportunity" became available as the former lineage gradually disappeared (fig.18,28,37). This situation seems to have triggered a repetitive response in R.bergonii which gave rise to a second lineage branching. Consequently, the changes observed in the three characters in R.sigmoida would most likely be nonrandom since iterative evolution in R.praebergonii, which based on the Range Test was nonrandom, was probably a result of selection for appropriate adaptive features for the vacated "niche". However, the temporal sequence in WC in R.praebergonii is consistent with a random walk. The probability of

generating two such temporally consecutive branching events in AL, HH and the WC purely by chance must be very low. However, the divergence of R.praebergonii from R.bergonii with regard to WC is not as obvious as between R.sigmoida and R.bergonii thus making this variable more questionable as far as consistency with a random walk is concerned.

Both AL and HH in R.bergonii indicate a nonrandom pattern of change based on the Range Test in almost all the cores in which it was sampled (table 20,21). The two exceptions are the temporal sequences of AL in the Indian Ocean and in core 504 in which the variable conforms to a random walk. The result in the Indian Ocean site is very hard to explain while the randomness in 504 is probably an artifact of the short time period over which R.bergonii was sampled. In the neighboring core 157, AL shows a highly significant anagenetic pattern of change which also would be expected in 504 since the two sites should be part of the same population. If R.bergonii in core 504 was sampled over the same time period as in 157 AL would probably exhibit a significant trend. The evolution of the length of the apical process in the central equatorial population (RC12-66 and 573) show a trend. However, the anagenetic pattern in 573 is a borderline case meaning that the x-value is just above the critical value of 2.25. This is also a case where the

change in AL should be interpreted as being anagenetic since R.bergonii in core RC12-66 and Site 573 belongs to the same panmictic population. The same explanation also pertains to the change in HH since the situation is similar; that is R.bergonii in RC12-66 is significantly in anagenesis for this character while in Site 573 it is a borderline case. The Indian Ocean population of R.bergonii did not evolve at all with respect to HH but instead it remained static throughout the sampled interval which may indicate that different environmental conditions prevailed in this part of the distribution range. Likewise, HH of R.bergonii was found to be significantly in stasis in Site 504 during the 0.5 m.y. period. On the other hand, HH changed significantly in 157. The width of the valve also changed in a nonrandom fashion in 157 but not in 504 (table 22); this leads me to think that the change in the WC in the eastern equatorial is also anagenetic because of being part of the same panmictic population. Similarly, I interpret the pattern of change in the WC in the central equatorial population where the temporal sequence in RC12-66 is consistent with a random walk but not in 573 (table 22). In the Indian Ocean core WC conforms to random walk which is also hard to explain since no other sites have been sampled within this population.

D. Patterns and rates of morphological change

As far as the temporal sequences of AL and HH in R.praebergonii and R.bergonii are concerned it should be pointed out that in at least one site within the three different water masses the null hypothesis of a random walk was rejected (tables 20,21). AL of R.bergonii in the Indian Ocean being the sole exception. All the three variables of R.sigmoida appear to be consistent with the null hypothesis while the time series of WC in R.praebergonii and R.bergonii are also questionable as far as indicating nonrandom temporal variation. I have also argued that the time sequences of the three variables are most likely nonrandom in R.praebergonii and R.bergonii because the "same event" (morphological divergence event) is found simultaneously in two semi-isolated populations which may be evidence for a common cause. Likewise, the divergence of R.sigmoida from R.bergonii as indicated by the three variables in Site 157 appears to have been repeated by R.praebergonii as R.sigmoida started to decline in abundance; this should be explained as an iterative adaptive response to an "ecological opportunity" rather than as chance. Consequently, there is a justification for believing that the morphological sequences in all lineages, despite the fact that the Range Test indicates that some of them conform with a random walk, exhibit largely nonrandom

variation.

There are some inconsistencies between the regression analyses of the variables which are not divided into distinct periods, and the Range Test. Those sequences that were subsectioned cannot be directly compared to the results of the Range Test since the latter was performed on whole temporal sequences while regression analysis was done separately on the subseries. However, the discrepancy is that in some cases the Range Test indicates anagenesis while the regression coefficient is not significantly different from zero which can be interpreted as stasis; the situation can also be reversed. For instance, each of the chronological sequence of AL and WC in R.praebergonii in the Indian Ocean site has a slope that does not differ significantly from zero while the Range Test indicates that anagenesis prevailed. Likewise, the time sequences of AL,HH and WC in R.bergonii show slopes consistent with stasis in core 573 when anagenesis dominated as based on the Range Test. These findings also apply to AL and HH in Site 157 as well as to HH in core RC12-66 while the situation was reversed for HH in the Indian Ocean core, that is the regression coefficient was significantly different from zero but the Range Test shows that stasis existed. These disagreements may be attributable to the significance of the regression coefficient being dependent upon the

number of samples used while the Range Test is insensitive to sample size (Fenster et al submitted). A similar explanation can also be offered to interpret the insignificant differences in slope between the first and second phase of evolution of AL and WC in Site 504 as well as for AL in V28-179.

Heterogeneity of regression slopes and/or intercepts with respect to geography for the recognized evolutionary stages of each variable in R.praebergonii, R.bergonii and R.sigmoida are in this study considered to indicate different patterns of change. This information is valuable because if there is geographic variation in temporal patterns of evolution within each lineage which is highly correlated to the water mass they occupied it may be interpreted as an indication of the existence of semi-isolated populations with regard to these regions. As far as this study is concerned R.praebergonii and R.bergonii were sampled from three different water systems (central equatorial, Peru water masses and Indian equatorial system) (fig. 10) between which the above lineages may not have been fully panmictic. If there existed different environmental conditions in the central and Indian equatorial water systems as well as in the Peru water mass which could have affected the evolution of R.praebergonii and R.bergonii from a genetic or a ecophenotypic point of view, variation in the temporal

pattern of change would be an expected outcome provided that the presumed populations were semi-isolated. In general, the Peru water body contains water which is cooler (Dinkleman 1973) than in the equatorial water mass and also exhibits a greater range of salinity (Collier 1970). These conditions are thought to have prevailed over the last 5 million years because there has been little change in the oceanography and topography in the region during this time period (Heath and van Andel 1973). Moreover, the equatorial current system is located further to the south in the Indian Ocean than it is in the Pacific Ocean (Collier 1970). The monsoons, which are typical of the Indian Ocean, create a surface circulation that alternates between southwest and northwest flows; this weather condition also gives rise to large influxes of fresh water and thus high variability in salinity (Collier 1970). Based on the environmental differences between the three water circulation systems it can be concluded that there is a potential for finding different patterns of evolution in each of the regions, if the gene flow was restricted. The analysis of covariance and the multiple comparison test of recognized stages of the three variables in R.praebergonii indicate that the Peru water mass represented a population which was partially isolated from a central equatorial population since the pattern of evolution is distinct in each of these regions

(tables 5-9). Moreover, the observation that R.sigmoida only occurred in the eastern equatorial Pacific Ocean and not in the central region (with the exception of a few samples in 573) lends further support to the idea that these two geographic areas were composed of two semi-isolated populations. The temporal sequences of all the variables in cores RC12-66,V28-179 and 573 in the central equatorial region estimate the same regression equation; in other words they can be grouped together as being one pattern (tables 5-9). On the other hand, AL and the early evolutionary stage of HH show an intermediate pattern of evolution in Site 572C with respect to the eastern and the central equatorial cores (table 5-7). Since this core was drilled in an area where the Peru water mass meets the central equatorial water system it can be inferred that the morphological evolution of R.praebergonii there was affected by migration from both semi-isolated populations and may thus be spurious. The temporal pattern of change of the three variables in R.praebergonii in the Indian Ocean core is not as distinct from the central equatorial which may be a result of total panmixis (table 5-9). In these arguments geographic variation is assumed to be maintained by and thus be an indicator of decreased migrational exchange between populations without considering simultaneous evolution and migration as a possibility.

There is no consistent temporal pattern in the three variables in R.bergonii (table 10-12). Only the pattern of change in HH in the Indian Ocean is distinct with regard to the other sites which from homogenous group. Both AL and WC in R.bergonii are difficult to interpret since geographic variation in the patterns of change are not related to the water masses.

E. Mode of evolution

In this study of tempo and mode in evolution, I have rephrased the original punctuated equilibrium hypothesis (Eldredge and Gould 1972;Gould and Eldredge 1977) in terms of character evolution. Consequently, the other extreme model or phyletic gradualism should also be interpreted as change in the frequency distribution of a particular trait in a population. The reason for redefining the hypothesis of punctuated equilibrium and phyletic gradualism is that there is not enough information present in this data set nor about present Rhizosolenia populations to know to what extent the morphological divergence between R.praebergonii and R.bergonii as well as R.sigmoida and R.bergonii reflected origination of new biological species.

The kinds of linear representations that were fitted to the morphological divergence events in this data set will lead to certain conclusions about the

relative frequency of punctuated character stasis (model 5) and phyletic character gradualism (model 8) as well as how these relate to each other temporally (fig. 39-41).

The initial "break" at approximately 3.1 Ma between R.praebergonii and R.bergonii for all three variables took place through a significant punctuation in 10 out of 12 possible cases (tables 23-24; fig. 58,59,61,63, 53,55,56,42,44,45). However, AL and HH in RC12-66 changed gradually during the incipient divergence event (fig.43,52). The same kind of situation was also found when R.sigmoida branched off from R.bergonii, that is only WC changed without a significant saltation, that is in 1 case out of 6 (tables 23-24; fig.48,49,50,51,60,62). Consequently, the predominant pattern of change during the divergence events in morphology is consistent with character punctuation. On the other hand, the pattern of change that took place after the initial "break" in the three lineages is not at all in agreement with the punctuated character stasis pattern. In both R.praebergonii and R.sigmoida AL,HH and WC continued to evolve in a gradual manner after the incipient character saltation as opposed to remaining in stasis. However, after the first appearance of R.praebergonii in the Indian Ocean core, AL remained static; consequently this can be considered to be an exception to the observation in the Pacific Ocean (tables 23;fig.58,53,42). As

R.praebergonii and R.sigmoida became established as distinct morphotypes (2.7 Ma and 3.1 Ma), the former remained static for all three characters in 7 cases out of 18 (including the cores where just R.praebergonii was sampled) while the latter showed stasis in the AL,HH and WC in 2 cases out of 6 (tables 23-24; fig.42-65). Consequently, character stasis, seems to be just about equally frequent as gradual character evolution. The ancestral lineage, R.bergonii, is expected to exhibit character stasis if it was to comply with the punctuated character stasis pattern which in fact occurred 11 times out of a possible 15.

The significant incipient saltations in morphology, which are very common in the investigated temporal sequences, are not at all the kinds of "breaks" (equated with a punctuation in this study) predicted by the punctuated equilibrium hypothesis since these did not give rise to distinct morphological entities in a geologically short period of time. Moreover, it is not known to what degree the quantified morphological changes reflect a speciation event; thus this study may not be a test of punctuated equilibrium as it was phrased by Eldredge and Gould (1972) but rather a study of rates and patterns of character evolution which may reflect a speciation event. Consequently, these types of character punctuations cannot be taken as corroborative evidence

for the punctuated equilibrium hypothesis. The initial shifts in morphology in R.praebergonii and R.sigmoida may be explained as reflecting a very short period of time when evolution was accelerated but not punctuated sensu Eldredge and Gould (1972). Another possible explanation for the significant breaks between R.praebergonii and R.bergonii as well as between R.sigmoida and R.bergonii is that they are artifacts of aggregation. This phenomenon, according to Bookstein et al. (1978), increases hidden randomness in temporal data and thus (character) punctuations should be interpreted with great caution. If these character saltations were in fact "real" (a period of accelerated evolution), which is not possible to determine in this case, the patterns are consistent with the weak version of punctuated character stasis which states that character evolution does not take place at a constant pace but varies through time. The fact that both R.praebergonii and R.sigmoida were nearly indistinguishable from R.bergonii around their first appearance as well as the presence of intermediate forms between ancestor and descendants support gradual phyletic change in the investigated characters. The only patterns consistent with punctuated character stasis in this data set, are the cases of character stasis in R.praebergonii and R.sigmoida after they became established as distinct morphotypes as well as in

R.bergonii. However, stasis and rapid evolutionary change in the fossil record is in no way inconsistent with phyletic evolution and it can also be explained by conventional Neo-Darwinian mechanisms (e.g.Charlesworth et al. 1982; Lande 1986). An exception to these observations are the "significant" breaks between R.praebergonii and R.bergonii in the Indian Ocean which gave rise to the former as a distinct lineage. However, there is evidence for this punctuation being an artifact of migration as well as for independent origination followed by parallel evolution. The migration hypothesis in conjunction with evolution is supported by the fact that the first appearance of R.praebergonii took place 200.000 years later in the Indian Ocean while the independent origination hypothesis is strengthened by the existence of R.praebergonii in the Indian Ocean as a distinct morphotype 200.000 years earlier than in the Pacific Ocean. If such an abrupt "break" in morphology was "real" (without intermediate forms) it would be very close to reflecting the extreme form of punctuated character stasis pattern which states that the majority of lineages remain in character equilibrium which is interrupted by abrupt changes in morphology (adopted from Hecht and Hoffman 1986). Such a pattern may also require special explanations in that the conventional mechanisms of Modern Synthesis would not be able to

account for such large gaps in such a short period of time.

The results of this analysis indicate that the patterns of evolution in R.praebergonii, R.sigmoida and R.bergonii represent different degrees of combinations of punctuated caharacter stasis and phyletic character gradualism rather than being dominated by either one of the extreme patterns (models 5 or 8). Similarly, Malmgren et al. (1983) found a pattern of evolution, which exhibits a long period of morphological stasis punctuated by relatively rapid gradual phyletic change, however, without resulting in lineage splitting, in the late Neogene planktonic foraminifera lineage Globoratalia tumida. Furthermore, these workers suggested that this pattern, which they call punctuated gradualism, may be a common norm of evolution in planktonic foraminifera (Malmgren et al. 1983).

F. Geographic/ecophenotypic variation and migration

The patterns of geographic variation of the three variables in R.praebergonii at the investigated temporal levels lends further support to the hypothesis that the central equatorial and the Peru water masses constitute semi-isolated populations of the above lineage. This is because the central equatorial sites tend to form a distinct morphological group with regard to the eastern

equatorial site (tables 25-30) which also was concluded from the analysis of covariation of the temporal pattern of mean change in AL,HH and the WC (tables 5-9). The status of the Indian Ocean as far as being a distinct population is concerned is uncertain, which also was the case when the temporal patterns were examined, since the characters of R.praebergonii show resemblance to the morphotypes in both the central and eastern equatorial Pacific at different time levels (tables 5-9). AL of R.bergonii separate the lineage into an eastern and a central equatorial form while the same variable in the Indian Ocean site indicate similarities with central equatorial region (tables 31-33). This of course support the idea that R.bergonii in the eastern equatorial population not being fully panmictic with the same lineage in the central equatorial region. On the other hand, both HH and WC show lack of pattern of geographic variation which then argue against the above hypothesis. An interesting aspect of these results is that two different types of analysis (Tukey's studentized range test and ANCOVA) bring forth essentially the same types of results as far as geographic variation is concerned, which probably could have been a result of different paleoenvironmental conditions in these regions (Collier 1970;Dinkleman 1973). However, it is impossible to infer whether the spatial variation in morphology is genetic or

nongenetic in nature as opposed to temporal change in a particular location, which is thought to be genetic in nature. These arguments are good indications of R.praebergonii and R.bergonii possibly having been composed of two semi-isolated populations;this assumes, which has also been pointed out earlier, that geographic variation is maintained by a restricted gene flow rather than migration in conjunction with morphological change.

Provided that the assumption of restricted gene flow holds the temporal patterns of morphological change in either location should not be severely confounded by for instance directional migration of geographic variants. However, Site 572C, which has an intermediate location between the two regions, is an exception since the morphological sequences there could have been affected by migration from both populations thus resulting in intermediate forms with respect to the two populations. In fact, this is what both analysis (ANCOVA and Tukey's test) bring forth as far as AL and HH of R.praebergonii is concerned. Consequently, it is likely that the patterns of temporal variation in morphology are flawed in Site 572C. An alternative explanation could be that the site was affected by the different environmental conditions which resulted in the unique geographic as well as temporal patterns in morphology. If the this idea was correct the unique position the site takes in terms

of patterns of spatial and temporal variation in mean morphology in R.praebergonii would be "real". There is also a possibility that both of the above factors were involved.

XIII. SUMMARY

Based on criteria for identifying ancestral-descendant relationships (Prothero and Lazarus 1980) it can be concluded that both R.praebergonii and R.sigmoida originated from R.bergonii in the equatorial Pacific Ocean via a morphological divergence event at 3.1 Ma and 3.3 Ma respectively. However, the branching event between R.sigmoida and R.bergonii was restricted only to the eastern equatorial region of the Pacific or the Peru water mass and it took place prior to the origination of R.praebergonii. The ancestral-descendant relationships are substantiated by the fact that at their first appearance both R.praebergonii and R.sigmoida were nearly indistinguishable from R.bergonii as far as the investigated characters are concerned. Through time, differences in morphology were enhanced due to a relatively rapid decrease in the length of the apical process,the height of the hyaline area and in the width of the valve of R.praebergonii and R.sigmoida whereas R.bergonii underwent a slight increase in the size of the corresponding characters. Moreover, R.bergonii is

stratigraphically positioned prior to the first appearance of both R.praebergonii and R.sigmoida and it is also found both during and after the divergence event in all the investigated sites; this lends further support for the ancestral-descendant relationships. As R.praebergonii and R.sigmoida became established as distinct morphotypes at around 2.7 Ma and 3.2 Ma respectively the morphology continued to change at a relatively slower rate until they disappeared at approximately 1.7 Ma and 3.0 Ma. The evolution of R.praebergonii in the eastern equatorial Pacific Ocean seems to have been iterative in the sense that it came to occupy the essentially the same "morphospace" which characterized R.sigmoida before it disappeared. The first appearance of R.praebergonii in the Indian Ocean took place 200.000 years later than in the Pacific Ocean. Based on such a step-wise pattern of first appearances in conjunction with the absence of intermediate morphologies between R.praebergonii and R.bergonii in the Indian Ocean ,the possibility of R.praebergonii migrating into the Indian Ocean after its origination in the Pacific Ocean arises. An alternative interpretation of the available data is that R.praebergonii evolved independently from R.bergonii in the Indian Ocean after which it underwent parallel evolution; this implies that "R.praebergonii" in the Indian and Pacific Ocean were actually two different

species.

The analysis of geographic variation in morphology at various time levels as well as temporal patterns of evolution, which may be due to environmental differences in the separate water masses, indicate that the Pacific Ocean may have been composed of two semi-isolated populations of R.praebergonii and R.bergonii. This is primarily supported by the fact that the central and eastern Pacific cores form two distinct groups with regard to morphology as well as by R.sigmoida being restricted only to the Peru water mass. However, this hypothesis assumes that geographic variation is maintained by a restricted gene flow between the two areas without evolution in conjunction with migration playing an important role. The status of the Indian Ocean site as far as being a semi-isolated population is concerned is inconclusive since R.praebergonii and R.bergonii in the Indian Ocean appears to show morphological affinity to the same lineages in the Pacific Ocean which may be due to total panmixis or simply lack of geographic variation.

Since the investigated diatom lineages most likely coexisted as well as were most likely restricted to the photic zone in the oceanic realm due to their dependency on photosynthetic activities, the branching events may have taken place according to the sympatric model in the

Pacific Ocean. This is further supported by the fact that intermediate morphologies are observed in all the Pacific core which would not be expected if lineage origination took place in allopatry or parapatry. A relative increase in the heavy oxygen isotope ^{18}O , which may have been a result of a cooling event in higher latitudes, coincides with the branching events. Biotic factors such as competition and predation are also discussed as possible factors which may have given rise to the morphological divergence. The relative importance of abiotic and biotic factors in triggering the morphological divergence event cannot be inferred.

With some exceptions both R.praebergonii and R.bergonii exhibited a nonrandom pattern of change in AL and HH within each population while the result with respect to WC is rather inconsistent. In addition, to the results of the Range Test (Bookstein 1987), the fact that the morphological divergence event took place simultaneously in two semi-isolated populations lends further support to the pattern of evolution being largely nonrandom. This is because the probability of such an event taking place at the same time in two semi-isolated purely by chance is very low. The same argument can be applied to the evolution of R.sigmoida, which according to the Range Test is consistent with a random walk, since iterative evolution, which is non-random in

R.praebergonii, (except WC), is highly unlikely to have happened just by chance alone. Thus, there could have been a common causal factor(s) involved. However, the status of the temporal sequence of WC in R.praebergonii and R.sigmoida is uncertain as far as randomness is concerned.

Based on fitting a set of hierarchical linear models, which describes punctuated character stasis and phyletic character gradualism as well as temporal combinations of these, to the temporal scatter of the data (Bookstein et al. 1978), it can be concluded that the origination of R.praebergonii and R.sigmoida from R.bergonii was consistent with phyletic character gradualism taking place possibly at varying rates rather than through punctuated character stasis (model 5) or the extreme version of character gradualism (model 8). This is because the significant morphological "breaks" did not give rise to distinct morphotypes in a geologically short time but it took place through a set of intermediate forms. Furthermore, phyletic evolution at varying rates is supported by the fact that both descendants were nearly indistuingshable from their ancestral form at their first appearances. On the other hand, the relative frequency of character stasis is rather high in particularly R.bergonii but also in R.sigmoida and R.praebergonii as they became established as distinct

morphotypes. These observations are the only ones that would be in agreement with the pattern of punctuated character stasis in the Pacific Ocean where the origination of the two morphotypes most likely took place. However, the significant character punctuations in R.praebergonii in the Indian Ocean are consistent with the punctuated character stasis pattern as opposed to the ones observed in the Pacific Ocean since this event gave rise to a distinct morphotype in a geologically short time. There is evidence for R.praebergonii migrating into the Indian Ocean as it originated in the Pacific Ocean as well as for independent evolution there. The former hypothesis is primarily supported by the later first appearance of R.praebergonii in the Indian Ocean while the latter idea is justified by the fact that R.praebergonii became a distinct morphotype earlier in the Indian Ocean as compared with the Pacific Ocean. Thus, the pattern observed in the Indian Ocean may be a "true" punctuated origination of a new morphotype or an artifact of migration.

XIV. CONCLUSION

The temporal patterns of morphological evolution in R.praebergonii, R.sigmoida and R.bergonii reflect a spectrum of combinations of phyletic character gradualism and punctuated character stasis, rather than being

dominated by either one of the extremes. Likewise, the geographic variability in the patterns of change among Indian, central Pacific and eastern Pacific Oceans shows a spectrum ranging from phyletic character gradualism to punctuated character stasis. Consequently, the claims about the history of life primarily being dominated by either punctuated character stasis or by phyletic character gradualism are in this case refuted. These findings may also suggest that that there is no need to rethink neo-Darwinian evolution since punctuated character stasis and phyletic character gradualism appear to be two extreme patterns, which describe fast and slow phyletic change, interconnected by a range of intermediate patterns rather than being mutually exclusive.

XV. APPENDICES

Appendix A.

Table 1. Rate of evolution in the length of the apical process (AL) in R.praebergonii. The slope (B) is in terms of microns per million years. $H_o: B_1 = B_2$ is the probability that the slope (B_1) before the "cut-point" is equal to the slope (B_2) after the "cut-point". $H_o: B_1 = 0$ and $H_o: B_2 = 0$ is the probability that the slope is zero prior to and after the cut point respectively. Within parenthesis are the 95% confidence intervals for the slopes.

SITE	CUT-POINT	B_1	B_2	$H_o: B_1 = B_2$	$H_o: B_1 = 0$	$H_o: B_2 = 0$
		(+,-3.13)	(+,-0.69)			
RC12-66	2.70	12.48	-0.85	P<0.001	P<0.001	P<0.01
		(+,-3.47)	(+,-30.8)			
V28-179	2.62	13.28	3.43	P>0.2	P<0.001	P>0.6
		(+,-5.63)	(+,-1.53)			
DSDP 573	2.68	14.35	-1.10	P<0.001	P<0.001	P>0.1
		(+,-5.17)	(+,-2.34)			
DSDP 572C	2.83	19.51	-2.51	P<0.001	P<0.001	P<0.03

Table 2. Rate of evolution in the height of the hyaline area (HH) in R.praebergonii. The slope (B) is in terms of microns per million years. $H_o: B_1 = B_2$ is the probability that the slope (B_1) before the "cut-point" is equal to the the slope (B_2) after the "cut-point". $H_o: B_1 = 0$ and $H_o: B_2 = 0$ is the probability that the slope is zero prior to and after the cut point respectively. Within parenthesis are the 95% confidence intervals for the slopes.

SITE	CUT-POINT	B_1	B_2	$H_o: B_1 = B_2$	$H_o: B_1 = 0$	$H_o: B2 = 0$
		(+,-1.0)	(+,-0.35)			
RC12-66	2.70	6.48	-0.02	P<0.001	P<0.001	P>0.9
		(+,-2.58)	(+,-9.38)			
V28-179	2.65	5.02	-2.14	P<0.05	P<0.001	P>0.4
		(+,-1.55)	(+,-0.41)			
DSDP 573	2.68	5.92	0.22	P<0.001	P<0.001	P>0.2
		(+,-1.28)	(+,-0.98)			
DSDP 572C	2.73	6.24	0.65	P<0.001	P<0.001	P>0.1
		(+,-1.71)	(+,-0.88)			
DSDP 157	2.75	5.46	-0.59	P<0.001	P<0.001	P>0.1

Table 3. Rate of evolution in the width of the valve (WC) in R.sigmoida. The slope (B) is in terms of microns per million years. $H_o: B_1 = B_2$ is the probability that the slope (B_1) before the"cut-point" is equal to the the slope (B_2) after the "cut-point". $H_o: B_1 = 0$ and $H_o: B_2 = 0$ is the probability that the slope is zero prior to and after the cut point respectively. Within parenthesis are the 95% confidence intervals for the slopes.

SITE	CUT-POINT	B_1	B_2	$H_o: B_1 = B_2$	$H_o: B_1 = 0$	$H_o: B2 = 0$
		(+,-8.68)	(+,-2.81)			
DSDP 157	3.28	22.39	-2.76	P<0.001	P<0.001	P<0.04
		(+,-37.5)	(+,-50.8)			
DSDP 504	3.14	23.04	0.48	P>0.1	P>0.07	P>0.9

Table 4. Rate of evolution in the length of the apical spine (AL) in R.sigmoida. The slope (B) is in terms of microns per million years. $H_o: B_1 = B_2$ is the probability that the slope (B_1) before the "cut-point" is equal to the the slope (B_2) after the "cut-point". $H_o: B_1 = 0$ and $H_o: B_2 = 0$ is the probability that the slope is zero prior to and after the cut point respectively. Within the parenthesis are the 95% confidence intervals for the slopes.

SITE	CUT-POINT	B_1	B_2	$H_o: B_1 = B_2$	$H_o: B_1 = 0$	$H_o: B2 = 0$
DSDP 157	3.28	(+,-21.4) 54.86	(+,-45.3) -0.31	P<0.001	P<0.001	P>0.4
DSDP 504	3.11	(+,-21,2) 35.12	(+,-37.2) 2.38	P>0.1	P<0.001	P>0.9

Table 5. Patterns of evolution in the length of the apical process (AL) in R.praebergonii. Overlapping 95% comparison limits of the slopes (b) and of the adjusted means of AL (adjusted for a common mean for time and a common regression line) for the sites indicate that the estimates of the regression coefficients and the intercepts (a) are the same (similar patterns). This is designated with the same grouping letter. Two or more grouping letters for a site indicate similarity to several distinct patterns of evolution.

$H_o: b_1 = b_2 = b_3 = b_4 = b_5 = b_6$, $P<0.001$; $H_o: a_1 = a_2 = a_3 = a_4 = a_5 = a_6$, $P<0.001$

SITE	INTERVAL (M.Y)	b 95% LIMITS	95% LIMITS ADJ.MEAN AL	GROUPS
IND.OC.	2.91-2.68	-10.053-7.725	15,083-13.253	C
RC12-66	3.11-2.70	8.152-16.818	16.764-15.340	A
V28-179	3.04-2.62	9.012-17.555	16.986-15.332	A
DSDP 573	3.02-2.68	8.606-20.104	16.767-15.189	A
DSDP 572C	3.17-2.83	13.800-25.214	14.94-13.119	B
DSDP 157	3.13-2.68	3.681-11.532	14.597-13.180	C

Table 6. Patterns of evolution in the length of the apical process (AL) in R.praebergonii. Overlapping 95% comparison limits of the slopes (b) and of the adjusted means of AL (adjusted for a common mean for time and a common regression line) for the sites indicates that the estimates of the regression coefficients and the intercepts (a) are the same (similar patterns). This is designated with the same grouping letter. Two or more grouping letters for a site indicate similarity to several distinct patterns of evolution.

$H_o: b_1 = b_2 = b_3 = b_4 = b_5 = b_6$, $P<0.005$; $H_o: a_1 = a_2 = a_3 = a_4 = a_5 = a_6$, $P<0.001$

SITE	INTERVAL (M.Y)	b 95% LIMITS	95% LIMITS ADJ.MEAN AL	GROUPS
IND.OC.	2.68-1.85	-4.613- -0.565	12.973-11.851	A
RC12-66	2.70-1.67	-2.312-0.807	13.351-12.167	A
V28-179	2.62-2.46	-17.74-13.49	14.187-12.109	A
DSDP 573	2.68-1.66	-2.892-0.554	13.402-12.084	A
DSDP 572C	2.83-2.04	-4.657-0.323	13.164-11.840	A B
DSDP 157	2.68-2.04	-0.078-5.928	11.845-10.580	B

Table 7. Patterns of evolution in the height of the hyaline area (HH) in R.praebergonii. Overlapping 95% comparison limits of the slopes (b) and of the adjusted means of HH (adjusted for a common mean for time and a common regression line) for the sites indicate that the estimates of the regression coefficients and the intercepts (a) are the same (similar patterns). This is designated with the same grouping letter in the left column. Two or more grouping letters for a site indicate similarity to several distinct patterns of evolution.

$H_o: b_1 = b_2 = b_3 = b_4 = b_5 = b_6$, $P<0.04$; $H_o: a_1 = a_2 = a_3 = a_4 = a_5 = a_6$, $P<0.001$

SITE	INTERVAL (M.Y)	b 95% LIMITS	95% LIMITS ADJ.MEAN HH	GROUPS
IND.OC.	2.91-2.68	4.642- -4.87	2.146-2.875	A B
RC12-66	3.11-2.70	8.377-4.600	2.363-2.897	A B
V28-179	3.04-2.65	7.316-2.733	2.132-2.787	A B
DSDP 573	3.02-2.68	8.465-3.374	2.653-3.251	A
DSDP 572C	3.17-2.73	8.240-4.249	1.797-2.428	B C
DSDP 157	3.13-2.75	7.681-3.238	1.380-1.943	C

Table 8. Patterns of evolution in the height of the hyaline area (HH) in R.praebergonii. Overlapping 95% comparison limits of the slopes (b) and of the adjusted means of HH (adjusted for a common mean for time and a common regression line) for the sites indicate that the estimates of the regression coefficients and the intercepts (a) are the same (similar patterns). This is designated with the same grouping letter in the left column. Two or more grouping letters for a site indicate similarity to several distinct patterns of evolution.

$H_o : b_1 = b_2 = b_3 = b_4 = b_5 = b_6$, $P<0.04$; $H_o : a_1 = a_2 = a_3 = a_4 = a_5 = a_6$, $P<0.001$

SITE	INTERVAL (M.Y)	b 95% LIMITS	95% LIMITS ADJ.MEAN HH	GROUPS
IND.OC.	2.68-1.85	0.993- -0.06	1.427-1.129	A B
RC12-66	2.70-1.67	0.395- -0.414	1.195-0.897	B C
V28-179	2.65-2.46	1.896- -4.516	1.499-1.015	A B
DSDP 573	2.68-1.66	0.614- -0.280	1.569-1.304	A
DSDP 572C	2.73-2.04	1.315- -0.255	1.343-0.996	A B
DSDP 157	2.75-2.04	0.081- -1.250	0.929-0.670	C

Table 9. Patterns of evolution in the width of the valve (WC) in R.praebergonii. Overlapping 95% comparison limits of the slopes (b) and of the adjusted means of WC (adjusted for a common mean for time and a common regression line) for the sites indicate that the estimates of the regression coefficients and the intercepts (a) are the same (similar patterns). This is designated with the same grouping letter in the left column. Two or more grouping letters for a site indicate similarity to several distinct patterns of evolution.

$H_o: b_1 = b_2 = b_3 = b_4 = b_5 = b_6$, $P<0.001$; $H_o: a_1 = a_2 = a_3 = a_4 = a_5 = a_6$, $P<0.001$

SITE	INTERVAL (M.Y)	b 95% LIMITS	95% LIMITS ADJ.MEAN WC	GROUPS
IND.OC.	2.91-1.85	-1.850- -3.896	7.944-7.130	B
RC12-66	3.11-1.67	-0.06- -1.523	8.610-7.866	A
V28-179	3.04-2.46	3.572- -0.775	8.671-7.604	A B
DSDP 573	3.02-1.66	-0.163- -1.840	8.646-7.925	A
DSDP 572C	3.17-2.04	-0.039- -1.981	8.271-7.400	A B
DSDP 157	3.13-2.04	-1.576- -0.091	7.271-6.588	C

Table 10. Patterns of evolution in the length of the apical process (AL) in R.bergonii. Overlapping 95% comparison limits of the slopes (b) and of the adjusted means of AL (adjusted for a common mean for time and a common regression line) for the sites indicate that the estimates of the regression coefficients and the intercepts (a) are the same (similar patterns). This is designated with the same grouping letter in the left column. Two or more grouping letters for a site indicate similarity to several distinct patterns of evolution.

$H_o: b_1 = b_2 = b_3 = b_4 = b_5$, $P<0.03$; $H_o: a_1 = a_2 = a_3 = a_4 = a_5$, $P<0.03$

SITE	INTERVAL (M.Y)	b 95% LIMITS	95% LIMITS ADJ.MEAN AL	GROUPS
IND.OC.	3.08-2.02	-0.488- -5.982	18.118-19.792	B C
RC12-66	3.37-1.67	2.329- -0.147	18.311-19.791	A
DSDP 573	3.28-1.66	0.957- -0.880	18.765-19.979	A B
DSDP 157	3.48-2.09	1.370- -1.113	18.102-19.207	A BC
DSDP 504	3.40-2.95	7.880- -7.223	16.769-18.750	C

Table 11. Patterns of evolution in the length of the height of the hyaline area (HH) in R.bergonii. Overlapping 95% comparison limits of the slopes (b) and of the adjusted means of HH (adjusted for a common mean for time and a common regression line) for the sites indicate that the estimates of the regression coefficients and the intercepts (a) are the same (similar patterns). This is designated with the same grouping letter in the left column. Two or more grouping letters for a site indicate similarity to several distinct patterns of evolution.

$H_o: b_1 = b_2 = b_3 = b_4 = b_5$, $P>0.1$; $H_o: a_1 = a_2 = a_3 = a_4 = a_5$, $P<0.001$

SITE	INTERVAL (M.Y)	b 95% LIMITS	95% LIMITS ADJ.MEAN HH	GROUPS
IND.OC.	3.08-2.02	-	5.859-5.159	B
RC12-66	3.37-1.67	-	4.328-3.740	A
DSDP 573	3.28-1.66	-	4.641-4.134	A
DSDP 157	3.48-2.09	-	4.216-3.770	A
DSDP 504	3.40-2.95	-	4.320-3.492	A

Table 12. Patterns of evolution in the width of the valve (WC) in R.bergonii. Overlapping 95% comparison limits of the slopes (b) and of the adjusted means of WC (adjusted for a common mean for time and a common regression line) for the sites indicate that the estimates of the regression coefficients and the intercepts (a) are the same (similar patterns). This is designated with the same grouping letter in the left column. Two or more grouping letters for a site indicate similarity to several distinct patterns of evolution.

$H_o: b_1 = b_2 = b_3 = b_4 = b_5$, $0.045 < P < 0.05$; $H_o: a_1 = a_2 = a_3 = a_4 = a_5$, $P < 0.001$

SITE	INTERVAL (M.Y)	b 95% LIMITS	95% LIMITS ADJ.MEAN WC	GROUPS
IND.OC.	3.08-2.02	-2.318-0.092	8.774-9.501	A
RC12-66	3.37-1.67	-0.525-0.561	9.151-9.763	A B
DSDP 573	3.28-1.66	-0.877-0.421	9.350-9.878	A B
DSDP 157	3.48-2.09	-1.411- -0.323	8.720-9.185	B
DSDP 504	3.40-2.95	-4.178-4.178	8.386-9.247	B

Table 13. Patterns of evolution in the length of the apical process (AL), height of the hyaline area (HH) and the width of the valve (WC) in R. sigmoida. Significant differences at the 5% level between slopes (b) and/or the intercepts (a) with respect to the sites is indicated by an asterisk (*).

COMPARED SITES	COMPARED INTERVAL (M.Y.)	VAR	$H_o: b_1 = b_2$	$H_o: a_1 = a_2$
157-504	3.35-3.28;3.23-3.11	AL	P>0.1	P<0.001*
157-504	3.28-3.07;3.11-2.92	AL	P>0.5	P>0.5
157-504	3.35-3.07;3.23-2.92	HH	P>0.08	P<0.004*
157-504	3.35-3.28;3.23-3.14	WC	P>0.9	P<0.001*
157-504	3.28-3.07;3.14-2.92	WC	P>0.2	P>0.2

Table 14. Patterns of evolution in the length of the apical process (AL) in R.praebergonii (P) and R.bergonii (B). Significant differences at the 5% level between slopes (b) and/or the intercepts (a) with respect to the two lineages is indicated by an asterisk (*).

SITE	TIME (MY) INTERVAL	a_P	a_B	b_P	b_B	$H_o: b_P = b_B$	$H_o: a_P = a_B$
IND.O.	2.91-1.85	14.3	30.4	-0.7	-4.4	P<0.001*	P<0.001*
RC12-66	3.11-2.70	-20.2	22.0	12.5	-0.9	P<0.001*	P<0.001*
DSDP573	3.02-2.68	-25.6	31.2	14.3	-4.3	P<0.001*	P<0.001*
DSDP157	3.13-2.04	-1.8	14.4	5.5	1.7	P<0.001*	P<0.001*
RC12-66	2.70-1.67	14.5	13.9	-0.7	2.2	P<0.001*	P<0.001*
DSDP573	2.68-1.66	15.4	12.3	-1.2	3.2	P<0.001*	P<0.001*

Table 15. Patterns of evolution in the height of the hyaline area (HH) in R.praebergonii (P) and R.bergonii (B). Significant differences at the 5% level between slopes (b) and/or the intercepts (a) with respect to the two lineages is indicated by an asterisk (*).

SITE	TIME (MY) INTERVAL	a_P	a_B	b_P	b_B	$H_o: b_P = b_B$	$H_o: a_P = a_B$
IND.O.	2.91-1.85	-0.7	9.2	0.9	-1.4	P<0.001*	P<0.001*
RC12-66	3.11-2.70	-16.4	8.9	6.5	-1.7	P<0.001*	P<0.001*
RC12-66	2.70-1.67	1.1	2.4	-0.0	0.8	P<0.003*	P<0.001*
DSDP573	3.02-2.68	-14.3	14.6	5.9	-3.6	P<0.001*	P<0.001*
DSDP573	2.68-1.66	1.0	2.9	0.2	0.7	P>0.1	P<0.001*
DSDP157	3.13-2.75	-14.2	7.5	5.4	-1.0	P<0.004*	P<0.001*
DSDP157	2.75-2.04	2.2	-0.5	-0.6	2.0	P<0.008*	P<0.001*

Table 16. Patterns of evolution in the width of the valve (WC) in R.praebergonii (P) and R.bergonii (B). Significant differences at the 5% level between slopes (b) and/or the intercepts (a) with respect to the two lineages is indicated by an asterisk (*).

SITE	TIME (MY) INTERVAL	a_P	a_B	b_P	b_B	$H_o: b_P = b_B$	$H_o: a_P = a_B$
IND.O.	2.91-1.85	14.6	12.6	-2.9	-1.3	P<0.05*	P<0.001*
RC12-66	3.11-1.67	10.2	9.4	-0.8	0.1	P<0.02*	P<0.001*
DSDP573	3.02-1.66	10.8	10.2	-1.0	-0.2	P>0.1	P<0.001*
DSDP157	3.13-2.04	5.0	11.1	0.7	-0.7	P<0.02*	P<0.001*

Table 17. Patterns of evolution in the length of the apical process (AL) in R.sigmoida (H) and R.bergonii (B). Significant differences at the 5% level between slopes (b) and/or the intercepts (a) with respect to the two lineages is indicated by an asterisk (*).

SITE	TIME (MY) INTERVAL	a_H	a_B	b_H	b_B	$H_o: b_H = b_B$	$H_o: a_H = a_B$
DSDP157	3.35-3.28	-167.6	-1.5	54.9	5.9	P<0.04*	P<0.001*
DSDP157	3.28-3.07	13.9	56.4	-0.3	11.8	P<0.004*	P<0.001*
DSDP504	3.23-3.11	-97.0	-58.8	35.1	24.3	P>0.2	P<0.001*
DSDP504	3.11-2.92	19.7	19.55	-2.4	-0.8	P>0.3	P<0.01*

Table 18. Patterns of evolution in the height of the hyaline area (HH) in R.sigmoida (H) and R.bergonii (B). Significant differences at the 5% level between slopes (b) and/or the intercepts (a) with respect to the two lineages is indicated by an asterisk (*).

SITE	TIME (MY) INTERVAL	a_H	a_B	b_H	b_B	$H_o: b_H = b_B$	$H_o: a_H = a_B$
DSDP157	3.35-3.07	-4.2	18.0	1.7	-4.4	P<0.005*	P<0.001*
DSDP504	3.23-2.92	-9.1	3.9	3.4	-0.1	P>0.05	P<0.001*

Table 19. Patterns of evolution in the width of the valve (WC) in R.sigmoida (H) and R.bergonii (B). Significant differences at the 5% level between slopes (b) and/or the intercepts (a) with respect to the two lineages is indicated by an asterisk (*).

SITE	TIME (MY) INTERVAL	a_H	a_B	b_H	b_B	$H_o: b_H = b_B$	$H_o: a_H = a_B$
DSDP157	3.35-3.28	-67.3	20.0	22.4	-3.4	P<0.002*	P<0.001*
DSDP157	3.28-3.07	13.7	18.2	-2.3	-3.0	P>0.8	P<0.001*
DSDP504	3.23-3.14	-66.0	-5.0	23.0	4.3	P>0.1	P<0.04*
DSDP504	3.14-2.92	6.0	15.6	0.1	-2.3	P>0.6	P<0.009*

Table 20. Results of the Range Test of the length of the apical process (AL). The reduced speeds are the expected deviations from starting size in AL (microns) under a random walk of one million years. The expected standard deviation (STD) in AL (microns) in one million years under a random walk. The "observed range" is the average range expressed in microns in AL throughout the investigated time interval. The calculated x statistic has a probability of $1-F(x^{-2})$ of leaving the range that is expected under a random walk.

SITE	LINEAGE	MEAN REDUCED SPEED	EXPT. STD	OBSERVED "RANGE"	x	$1-F(x^{-2})$	RESULT
IND.O.	R.praeb.	2.67	3.35	10.26	3.15	0.997	Anag.
RC12-66	R.praeb.	1.88	2.35	10.26	5.23	0.9999	Anag.
V28-179	R.praeb.	4.42	5.54	11.57	1.59	0.774	R.W.
DSDP573	R.praeb.	3.84	4.81	6.94	1.68	0.813	R.W.
DSDP572C	R.praeb.	4.14	5.19	7.30	1.49	0.731	R.W.
DSDP157	R.praeb.	4.71	5.90	14.08	2.49	0.976	Anag.
IND.O.	R.berg.	3.07	3.84	5.3	1.42	0.685	R.W.
RC12-66	R.berg.	2.60	3.26	6.14	2.46	0.971	Anag.
DSDP573	R.berg.	2.49	3.12	5.22	2.13	0.931	R.W/An.
DSDP157	R.berg.	7.13	8.93	23.85	3.14	0.997	Anag.
DSDP504	R.berg.	5.13	6.43	9.6	1.0	0.370	R.W.
DSDP157	R.sigm.	5.02	6.29	19.29	1.62	0.794	R.W.
DSDP504	R.sigm.	4.81	6.03	8.09	1.26	0.584	R.W.

Table 21. Results of the Range Test of the height of the hyaline height (HH). The reduced speeds are the expected deviations from starting size in HH (microns) under a random walk of one million years. The expected standard deviation (STD) in HH (microns) in one million years under a random walk. The "observed range" is the average range expressed in microns in HH throughout the investigated time interval. The calculated x statistic has a probability of $1-F(x^{-2})$ of leaving the range that is expected under a random walk.

SITE	LINEAGE	MEAN REDUCED SPEED	EXPT. STD	OBSERVED "RANGE"	x	$1-F(x^{-2})$	RESULT
IND.O.	R.praeb.	0.91	1.13	3.33	3.02	0.994	Anag.
RC12-66	R.praeb.	1.15	1.44	4.91	4.09	0.9999	Anag.
V28-179	R.praeb.	2.34	2.93	7.29	1.90	0.881	R.W.
DSDP573	R.praeb.	1.11	1.39	3.34	2.80	0.990	Anag.
DSDP572C	R.praeb.	1.42	1.78	2.64	1.58	0.774	R.W.
DSDP157	R.praeb.	1.24	1.56	5.80	3.88	0.9998	Anag.
IND.O.	R.berg.	1.68	2.10	1.08	0.53	0.985	Stas.
RC12-66	R.berg.	1.89	2.37	5.96	3.28	0.998	Anag.
DSDP573	R.berg.	1.94	2.43	4.04	2.12	0.931	R.W/An.
DSDP157	R.berg.	3.22	4.04	12.19	3.56	0.9992	Anag.
DSDP504	R.berg.	2.24	2.81	2.16	0.52	0.012	Stas.
DSDP157	R.sigm.	1.31	1.65	3.58	1.15	0.505	R.W.
DSDP504	R.sigm..	2.39	2.99	3.68	0.68	0.09	R.W.

Table 22. Results of the Range Test of the width of the valve (WC). The reduced speeds are the expected deviations from starting size in WC (microns) under a random walk of one million years. The expected standard deviation (STD) in WC (microns) in one million years under a random walk. The "observed range" is the average range expressed in microns in WC throughout the investigated time interval. The calculated x statistic has a probability of $1-F(x^{-2})$ of leaving the range that is expected under a random walk.

SITE	LINEAGE	MEAN REDUCED SPEED	EXPT. STD	OBSERVED "RANGE"	x	$1-F(x^{-2})$	RESULT
IND.OC.	R.praeb.	2.80	3.51	8.70	2.55	0.98	Anag.
RC12-66	R.praeb.	1.85	2.31	3.18	1.65	0.83	R.W.
V28-179	R.praeb.	2.39	2.99	4.22	1.08	0.437	R.W.
DSDP573	R.praeb.	2.23	2.80	3.78	1.57	0.774	R.W.
DSDP572C	R.praeb.	3.23	4.04	12.28	3.23	0.9977	Anag.
DSDP157	R.praeb.	3.26	4.08	6.80	1.74	0.834	R.W.
IND.OC.	R.berg.	1.67	2.09	2.25	1.11	0.478	R.W.
RC12-66	R.berg.	1.42	1.77	2.65	1.94	0.895	R.W.
DSDP573	R.berg.	2.14	2.68	8.36	3.97	0.9998	Anag.
DSDP157	R.berg.	3.54	4.44	8.93	2.37	0.964	Anag.
DSDP504	R.berg.	3.08	3.86	5.54	0.96	0.345	R.W.
DSDP157	R.sigm.	2.12	2.66	5.21	1.04	0.4	R.W.
DSDP504	R.sigm.	3.38	4.24	6.52	0.85	0.235	R.W.

Table 23. The best "fitting" linear representations of evolution of the length of the apical process (AL),height of the hyaline area (HH) and the width of the valve (WC) in R.praebergonii,R.bergonii and R.sigmoida. The r^2 is the coefficient of determination or the proportion of variance explained by the model chosen. N is the number of specimens measured for AL,HH and WC in each site. An asterisk (*) for site 157 indicate R.sigmoida and R.bergonii combination.

SITE	VARIABLE	N	MODEL	SUM-OF-SQUARES	r^2
IND.OC.	AL	965	10	8761.9	0.7361
RC12-66	AL	1123	14	8506.3	0.8012
V28-179	AL	370	2	1548.4	0.6581
DSDP 573	AL	1191	13	10127.7	0.7781
DSDP 572C	AL	509	4	1629.6	0.6216
DSDP 157	AL	1422	9	13896.1	0.7201
DSDP 157*	AL	1303	13	8003.4	0.7084
DSDP 504	AL	362	13	1674.7	0.6880
IND. OC.	HH	952	11	3710.5	0.8029
RC12-66	HH	1095	12	2086.4	0.7973
DSDP 573	HH	1066	16	1909.4	0.7564
DSDP 572C	HH	506	4	346.3	0.6952
DSDP 157	HH	1384	13	2690.2	0.8039
DSDP 157*	HH	1274	11	1406.2	0.6773

Table 24. The best "fitting" linear representations of evolution in the length of the apical process (AL),height of the hyaline area (HH) and the width of the valve (WC) in R.praebergonii,R.bergonii and R.sigmoida. Symbols as in table 23.

SITE	VARIABLE	N	MODEL	SUM-OF-SQUARES	r^2
DSDP 504	HH	355	13	442	0.7536
IND.OC.	WC	604	11	645.2	0.4859
RC12-66	WC	997	16	500.7	0.3585
V28-179	WC	365	1	28.57	0.0659
DSDP 573	WC	1061	9	510.0	0.3071
DSDP 572C	WC	489	1	92.75	0.1136
DSDP 157	WC	1203	11	1083.1	0.3904
DSDP 157*	WC	1036	16	1051.5	0.6141
DSDP 504	WC	226	15	206.3	0.5026

Table 25. Pattern of geographic variation in the mean length of the apical process (AL) in R.praebergonii. Sites that have the same grouping letter at a particular time level do not have significantly different means at the 5% level and thus form homogenous groups. Two or more letters indicate that a site have a mean AL that is similar to two or more groups. An asterisk (*) indicate the presence of a paleomagnetic reversal.

TIME LEVEL(MY)	IND.OC.	RC12-66	V28-179	573	572C	157
3.07*	-	A	A	A	B	B
3.04-3.02	-	B	A	A	C	C
2.99-2.98*	-	A	A	A	B	B
2.92-2.91*	B	A	A	A	B	B
2.84-2.82	C	A	A	A	C	B
2.76-2.74	A	A	A	A	B	B
2.69-2.66	B	B	B,A	B	-	A
2.59-2.58	C	A,B	A	A	-	B
2.53-2.49	C	B	A	B	_	C,B
2.47-2.45*	A,B	A	A	A,B	A,B	B
2.41-2.37	A	A	_	A	_	B
2.31-2.32	A	-	-	A	A	B
2.22-2.19	_	A,B	_	B,C	A	C

Table 26. Pattern of geographic variation in the mean length of the apical process (AL) in R.praebergonii. Sites that have the same grouping letter at a particular time level do not have significantly different means at the 5% level and thus form homogenous groups. Two or more letters indicate that a site have a mean AL that is similar to two or more groups. An asterisk (*) indicate the presence of a paleomagnetic reversal.

TIME LEVEL(MY)	IND.OC.	RC12-66	V28-179	573	572C	157
2.12-2.09	A	A	-	A	A	A
2.03-2.00	B	A,B	-	A	A	C
1.89-1.88*	A	B	_	B	-	-
1.67-1.66*	-	A	-	A	-	-

Table 27. Pattern of geographic variation in the mean height of the hyaline area (HH) in R.praebergonii. Sites that have the same grouping letter at a particular time level do not have significantly different means at the 5% level and thus form homogenous groups. Two or more letters indicate that a site have a mean HH that is similar to two or more groups. An asterisk (*) indicate the presence of a paleomagnetic reversal.

TIME LEVEL(MY)	IND.OC.	RC12-66	V28-179	573	572C	157
3.07*	-	A	A	A	B	B
3.04-3.02	-	B	A	A	B	C
2.99-2.98*	-	B	C	B	C	C
2.92-2.91*	A,B	A,B	A,B	A	B	B
2.84-2.82	B,C,D	A,B	C,B	A	D	C,D
2.76-2.74	A	B	B	A	B	C
2.69-2.66	A	B	B	B,A	-	B
2.59-2.58	B	B,C	B	A	-	C
2.53-2.49	A	B	A	A	-	B
2.47-2.45*	B	B	A	A	A	C
2.41-2.37	A	A	-	A	A	A
2.31-2.30	B	-	-	A	B	C
2.22-2.19	-	A	-	A	A	A

Table 28. Pattern of geographic variation in the mean height of the hyaline area (HH) in R.praebergonii. Sites that have the same grouping letter at a particular time level do not have significantly different means at the 5% level and thus form homogenous groups. Two or more letters indicate that a site have a mean HH that is similar to two or more groups. An asterisk (*) indicate the presence of a paleomagnetic reversal.

TIME LEVEL(MY)	IND.OC.	RC12-66	V28-179	573	572C	157
2.12-2.09	B	B	-	A	B	A,B
2.03-2.00	B,C	B,A,C	-	A	A,B	C
1.89-1.88*	A	B	-	B	-	-
1.67-1.66	-	A	-	A	-	-

Table 29. Pattern of geographic variation in the mean width of the valve (WC) in R.praebergonii. Sites that have the same grouping letter at a particular time level do not have significantly different means at the 5% level and thus form homogenous groups. Two or more letters indicate that a site have a mean WC that is similar to two or more groups. An asterisk (*) indicate the presence of a paleomagnetic reversal.

TIME LEVEL(MY)	IND.OC.	RC12-66	V28-179	573	572C	157
3.07*	-	B,C	B,A	B,C	A	C
3.04-3.02	-	A	B,A	B,C	A	C
2.99-2.98*	-	A	A	B,A	B,C	C
2.92-2.91*	C	A	A	A	B	C,B
2.84-2.82	B,C	B,A,C	B,A	A	C B	A,C
2.76-2.74	B,C	A	A	A,B	C,D	D
2.69-2.66	A	A	A	A	-	A
2.59-2.58	B	A	A	A	-	A
2.53-2.49	B	B,A	B,A	A	-	B
2.47-2.45*	A	A	A	A	A	B
2.41-2.37	B	A	-	A	-	B
2.31-2.30	B	-	-	A	B	C
2.22-2.19	-	A	-	A	A	C
2.12-2.09	B,A	A	-	A	B,A	B

Table 30. Pattern of geographic variation in the mean width of the valve (WC) in R.praebergonii. Sites that have the same grouping letter at a particular time level do not have significantly different means at the 5% level and thus form homogenous groups. Two or more letters indicate that a site have a mean WC that is similar to two or more groups. An asterisk (*) indicate the presence of a paleomagnetic reversal.

TIME LEVEL(MY)	IND.OC.	RC12-66	V28-179	573	572C	157
2.03-2.00	A	A	-	A	A	B
1.89-1.88*	A	B	-	A	-	-
1.66-1.67	-	A	-	A	-	-

Table 31. Pattern of geographic variation in the mean length of the apical process (AL) in R.bergonii. Sites that have the same grouping letter at a particular time level do not have significantly different means at the 5% level and thus form homogenous groups. Two or more letters indicate that a site have a mean AL that is similar to two or more groups. An asterisk (*) indicate the presence of a paleomagnetic reversal.

TIME LEVEL(MY)	IND.OC.	RC12-66	573	157	504
3.41-3.37*	-	A	-	B	B
3.26-3.25	-	A	-	B	B
3.30-3.28	-	-	A	B	B
3.21-3.18*	-	A	-	A	A
3.14-3.13	-	-	A	B	B
3.11-3.08*	A	A,B	A,B	B	C
3.07-3.06	-	A	A	A	-
3.04-3.02	-	A	A	A	-
2.98-2.96	A	-	A,B	A,B	B
2.76-2.73	A	B	A,B	A,B	-
2.41-2.37	A	A	A	B	_
2.24-2.25	A	-	A	B	-

Table 32. Pattern of geographic variation in the mean height of the hyaline area (HH) in R.bergonii. Sites that have the same grouping letter at a particular time level do not have significantly different means at the 5% level and thus form homogenous groups. Two or more letters indicate that a site have a mean HH that is similar to two or more groups. An asterisk (*) indicate the presence of a paleomagnetic reversal.

TIME LEVEL(MY)	IND.OC.	RC12-66	573	157	504
3.41-3.37*	-	A	-	B	A
3.26-3.25	-	A	-	A	A
3.30-3.28	-	-	A	B	B
3.21-3.18*	-	A	-	A	A
3.14-3.13	-	-	A	A	A
3.11-3.08*	A	B	B	B	B
3.07-3.06	-	A	A	A	-
3.04-3.02	-	A	B	B	-
2.98-2.96	A	-	B	B	B
2.76-2.73	A	B	A,B	A,B	-
2.41-2.37	A	B	A,B	C	-
2.24-2.25	A	-	B	C	-

Table 33. Pattern of geographic variation in the mean width of valve (WC) in R.bergonii. Sites that have the same grouping letter at a particular time level do not have significantly different means at the 5% level and thus form homogenous groups. Two or more letters indicate that a site have a mean WC that is similar to two or more groups. An asterisk (*) indicate the presence of a paleomagnetic reversal.

TIME LEVEL(MY)	IND.OC.	RC12-66	573	157	504
3.41-3.37*	-	A	-	B	B
3.30-3.28	-	-	A	A	A
3.26-3.25	-	A	-	A	A
3.21-3.18*	-	A	-	B	B
3.14-3.13	-	-	A	A	A
3.11-3.08*	A,B	A	A	A,B	B
3.07-3.06	-	A	A	A	-
3.04-3.02	-	A	A	B	-
2.98-2.96	A,B	-	A	B	B
2.76-2.73	A	A	A	A	-
2.41-2.37	A	A	A	A	-
2.24-2.25	A	-	A	A	-

Table 34. Rate of evolution in the length of the apical process (AL), the height of the hyaline area (HH) and the width of the valve (WC). The slope (B) is expressed in terms of microns per million years. H_o:B=0 is the probability that the slope is equal to zero. Within parenthesis are the 95% confidence intervals for the slopes

SITE	INTERVAL (M.Y.)	LINEAGE	VARIABLE	B	H_o:B=0
IND.OC.	2.91-1.85	R.praeb.	AL	(+,-1.06) -0.68	P>0.1
DSDP 157	3.13-2.04	R.praeb.	AL	(+,-1.45) 5.52	P<0.001
IND.OC.	2.91-1.85	R.praeb.	HH	(+,-0.43) 0.91	P<0.001
IND.OC.	2.91-1.85	R.praeb.	WC	(+,-0.84) -2.87	P<0.001
RC12-66	3.11-1.67	R.praeb.	WC	(+,-0.60) -0.79	P<0.001
V28-179	3.04-2.46	R.praeb.	WC	(+,-1.90) 1.40	P>0.1
DSDP 573	3.02-1.66	R.praeb.	WC	(+,-0.68) -1.0	P<0.001
DSDP 572C	3.17-2.04	R.praeb.	WC	(+,-0.80) -1.0	P<0.001
DSDP 157	3.13-2.04	R.praeb.	WC	(+,-0.67) 0.74	P<0.03
IND.OC.	3.08-2.02	R.berg.	AL	(+,-2.53) -3.23	P<0.001
RC12-66	3.37-1.67	R.berg.	AL	(+,-1.09) 1.10	P<0.04
DSDP 573	3.28-1.66	R.berg.	AL	(+,-1.29) 0.04	P>0.9
DSDP 157	3.48-2.09	R.berg.	AL	(+,-1.06) 0.13	P>0.8

Table 35. Rate of evolution in the length of the apical process (AL), the height of the hyaline area (HH) and the width of the valve (WC). The slope (B) is expressed in terms of microns per million years. (H_o:B=0) The probability that the slope is equal to zero. Within parenthesis are the 95% confidence intervals for the slopes.

SITE	INTERVAL (M.Y.)	LINEAGE	VARIABLE	B	H_o:B=0
DSDP 504	3.40-2.95	R.berg.	AL	(+,-7.30) 0.33	P>0.9
IND.OC.	3.08-2.02	R.berg.	HH	(+,-1.08) -1.25	P<0.02
RC12-66	3.37-1.67	R.berg.	HH	(+,-0.46) 0.00	P>0.9
DSDP 573	3.28-1.66	R.berg.	HH	(+,-0.54) -0.24	P>0.3
DSDP 157	3.48-2.09	R.berg.	HH	(+,-0.45) -0.50	P<0.03
DSDP 504	3.40-2.95	R.berg.	HH	(+,-3.10) 1.02	P>0.4
IND.OC.	3.08-2.02	R.berg.	WC	(+,-1.10) -1.11	P<0.04
RC12-66	3.37-1.67	R.berg.	WC	(+,-0.46) 0.02	P>0.9
DSDP 573	3.28-1.66	R.berg.	WC	(+,-0.56) -0.23	P>0.4
DSDP 157	3.48-2.09	R.berg.	WC	(+,-0.45) -0.88	P<0.001
DSDP 504	3.40-2.95	R.berg.	WC	(+,-3.20) -0.88	P>0.5
DSDP 157	3.35-3.07	R.sigmoida	HH	(+,-1.54) 1.73	P<0.02
DSDP 504	3.23-2.95	R.sigmoida	HH	(+,-3.82) 3.56	P<0.001

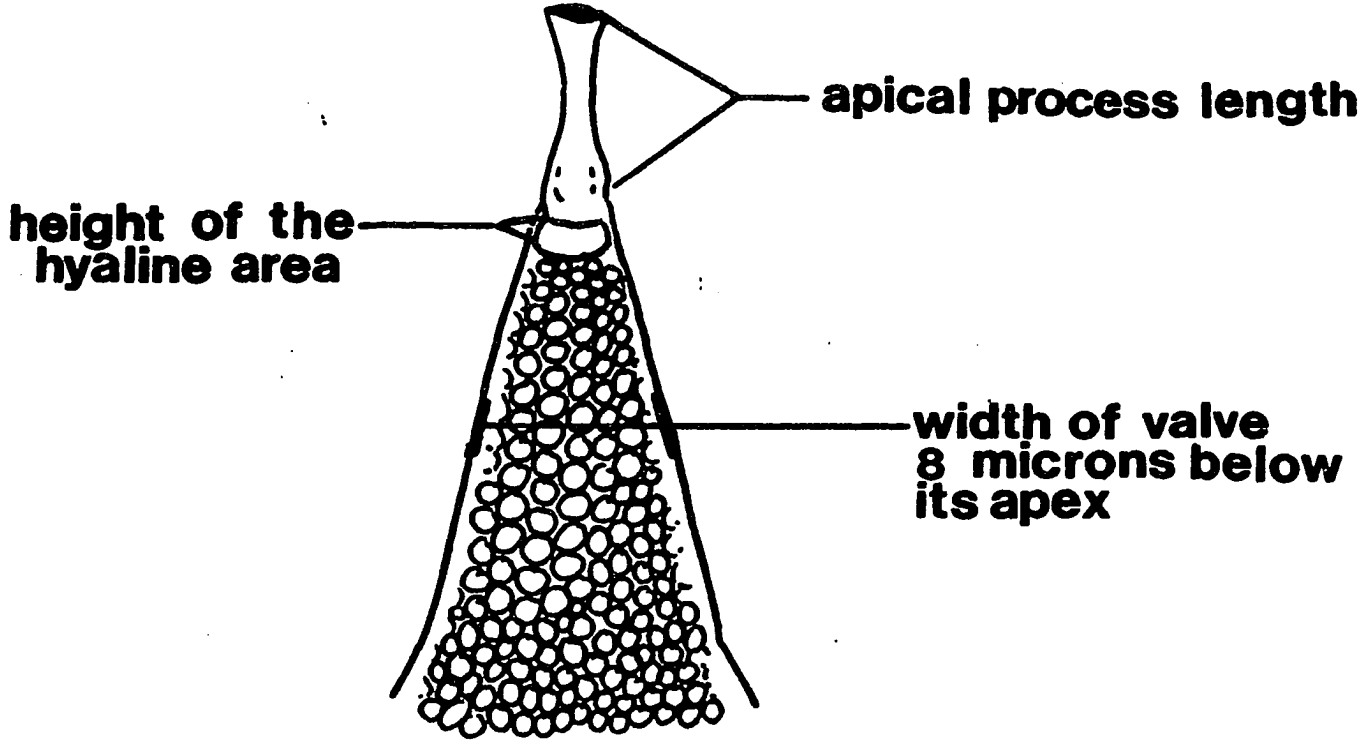


Figure 1 . Schematic diagram of the genus Rhizosolenia showing the parts that were measured.

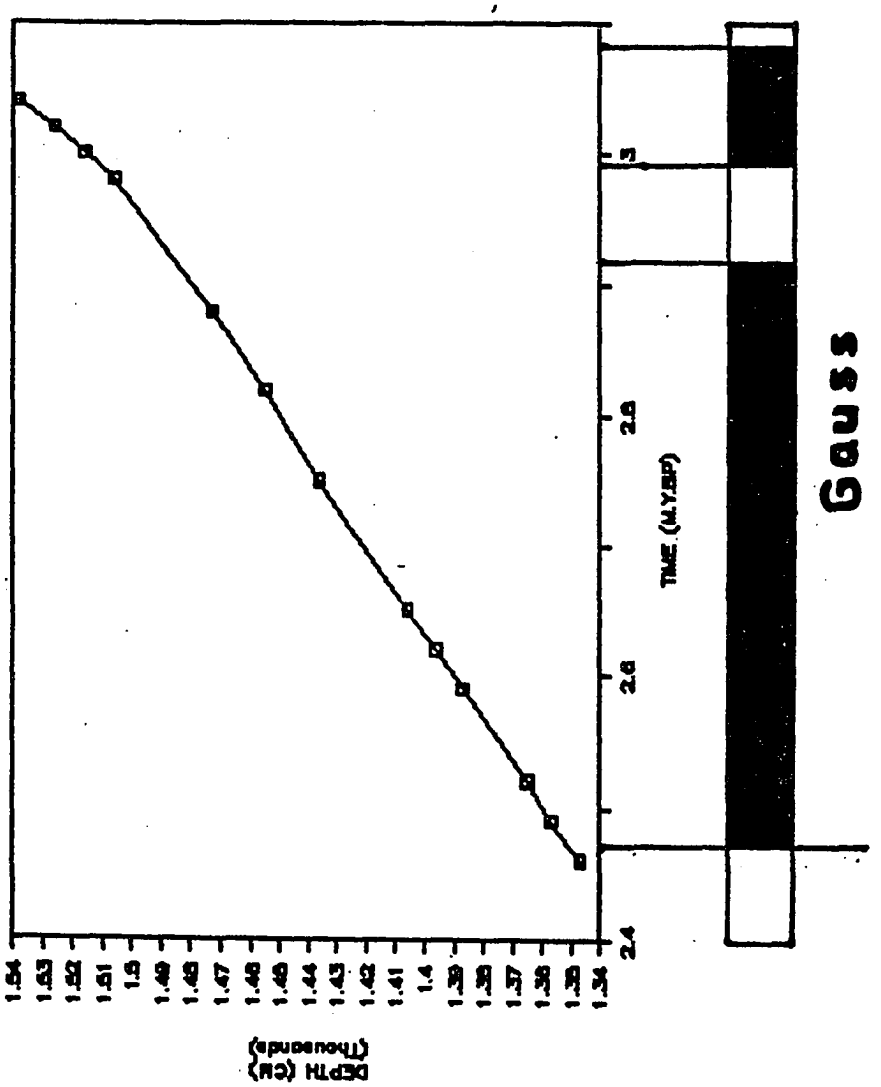


Figure 2. Depth vs. Time plot for V28-179.

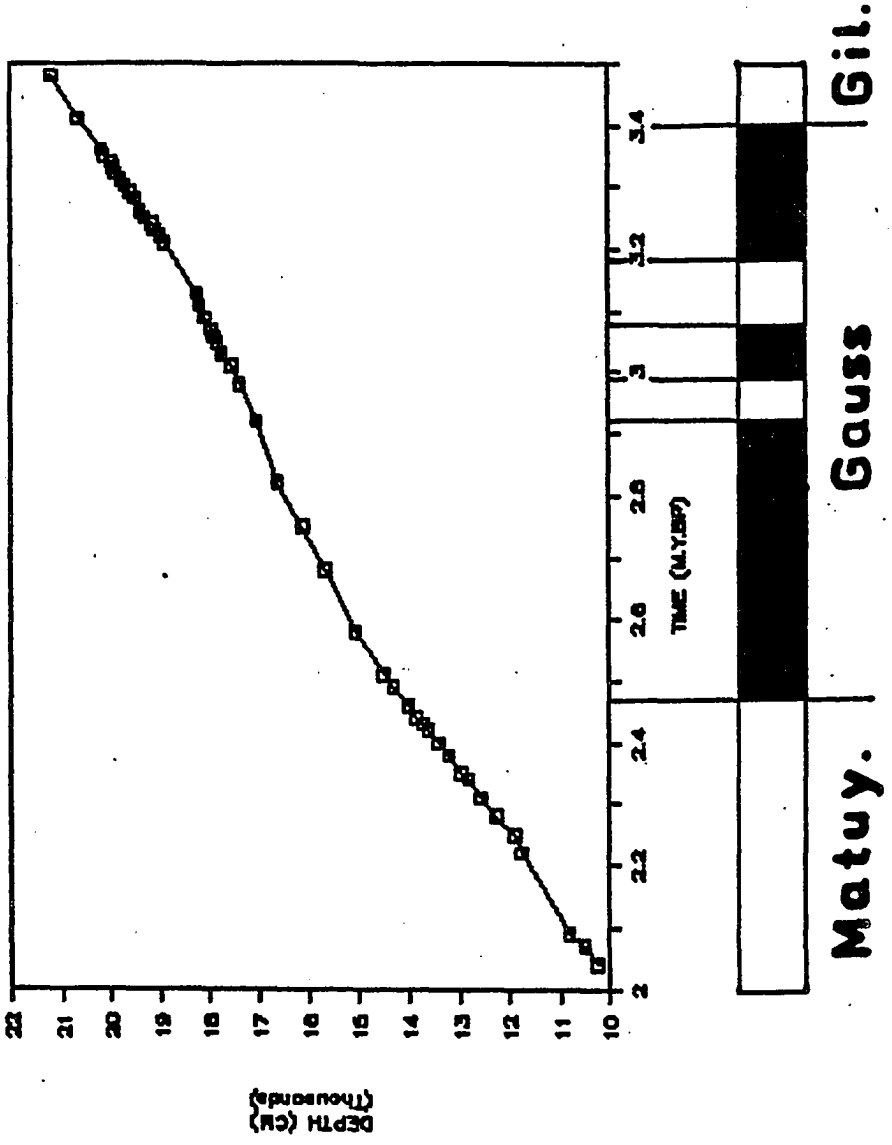


Figure 3. Depth vs. Time plot for DSDP site 157.

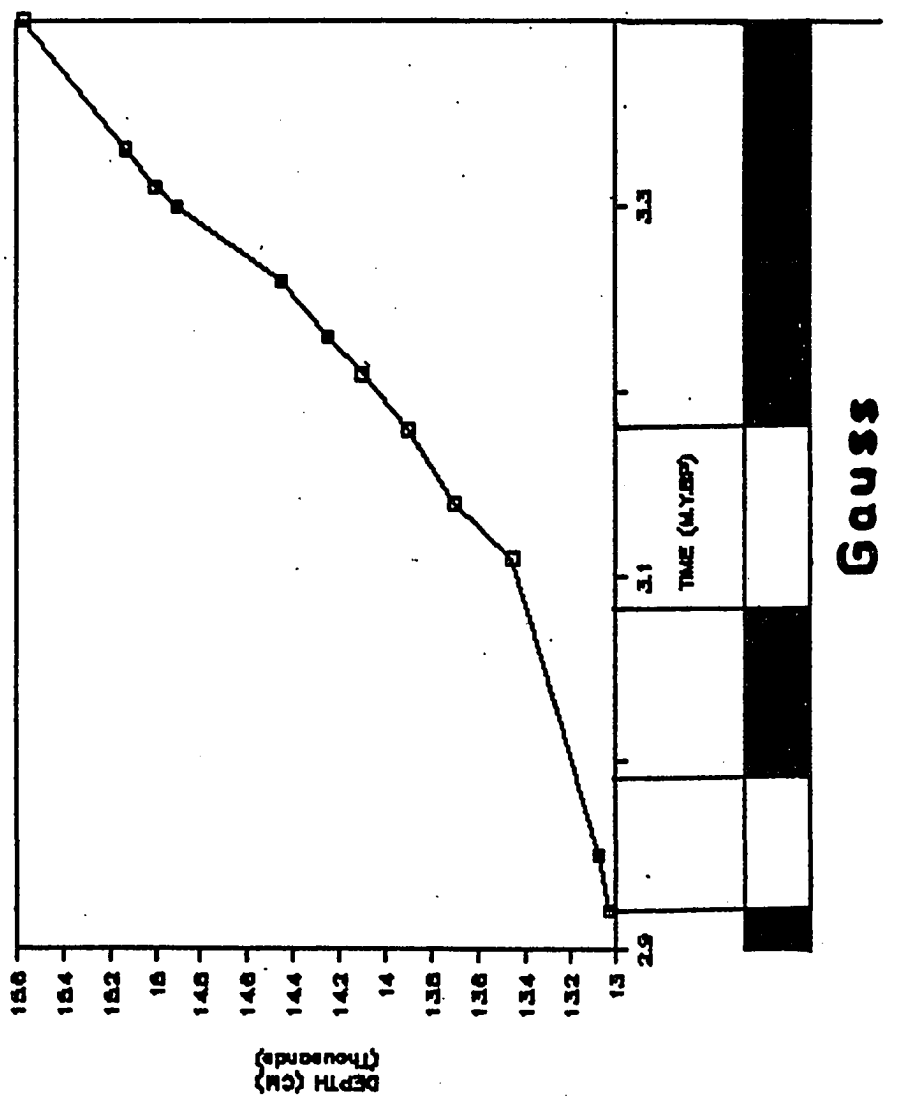


Figure 4. Depth vs. Time plot for DSDP site 504.

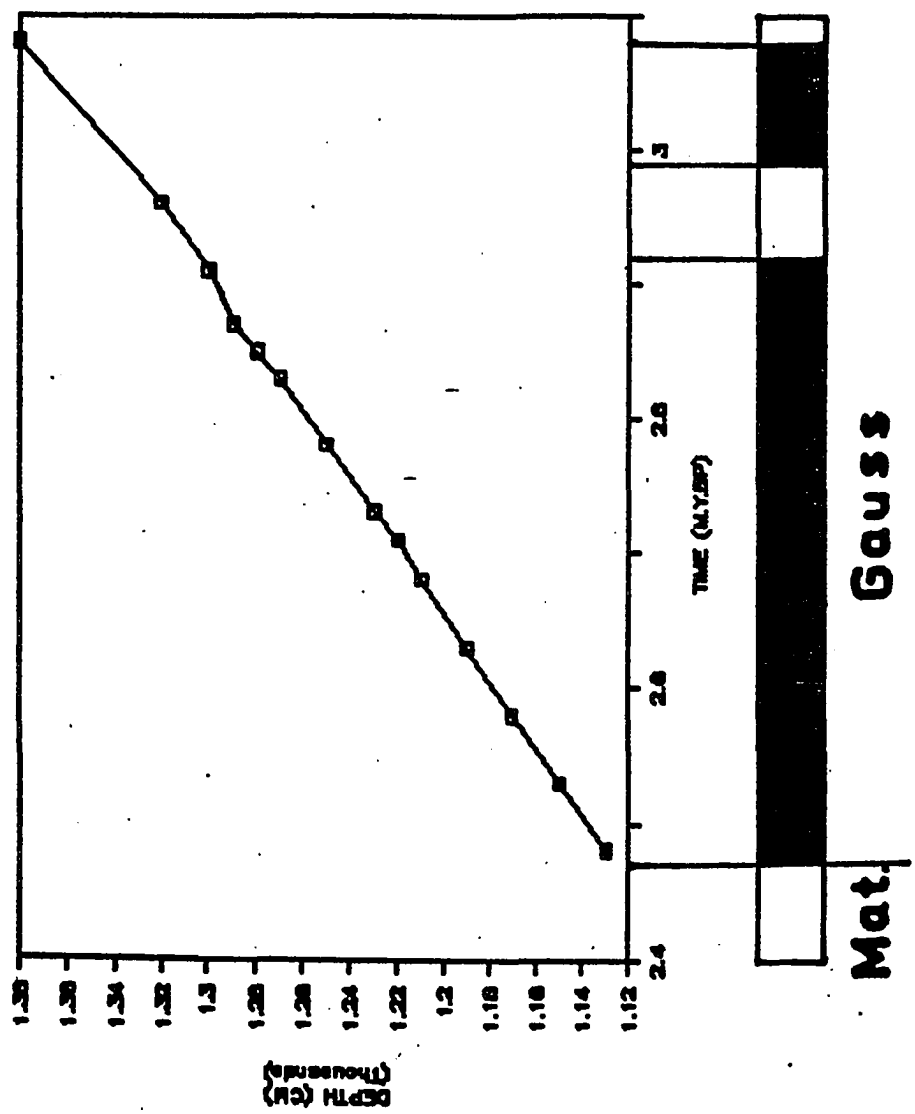


Figure 5a. Depth vs. Time plot for site V29-40.

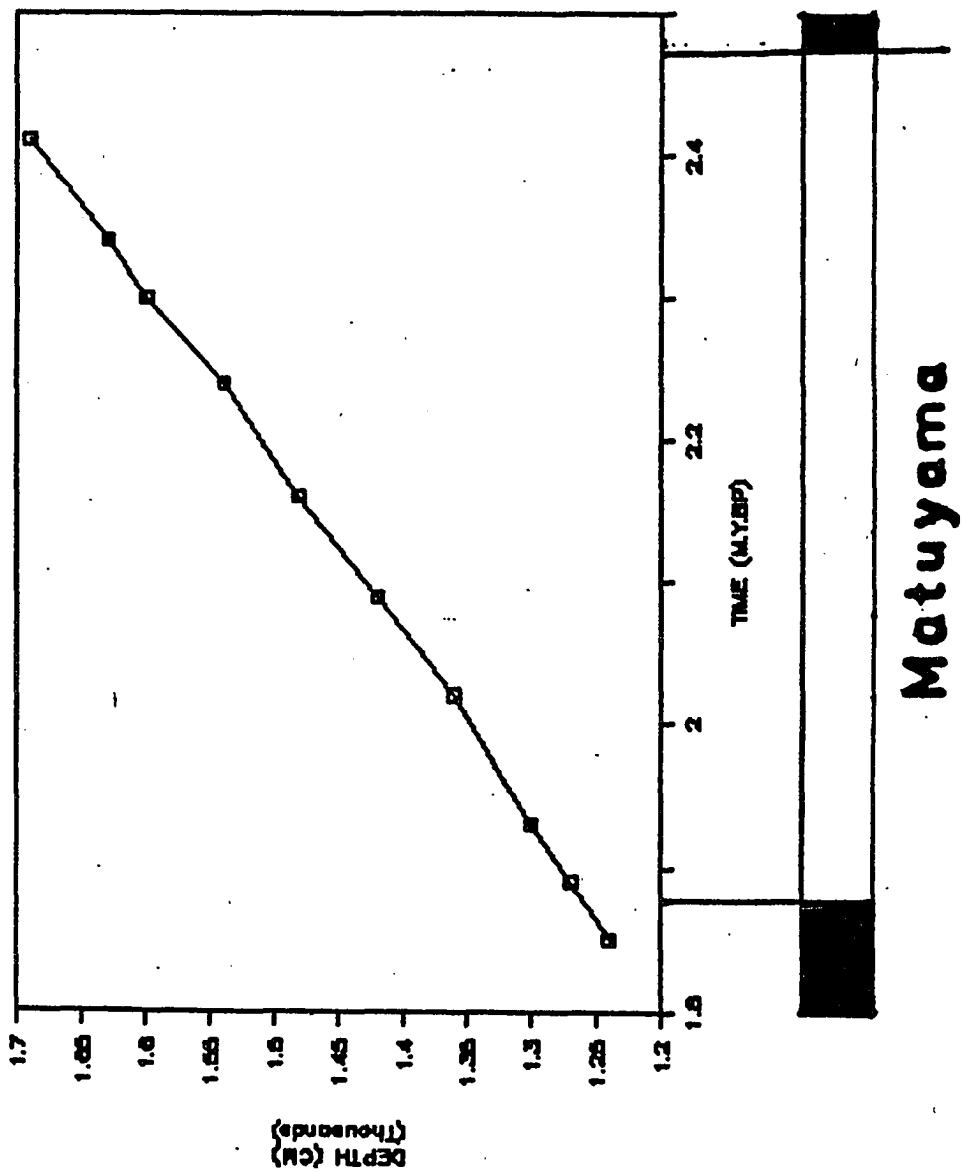


Figure 5b. Depth vs. Time plot for site RC14-22.

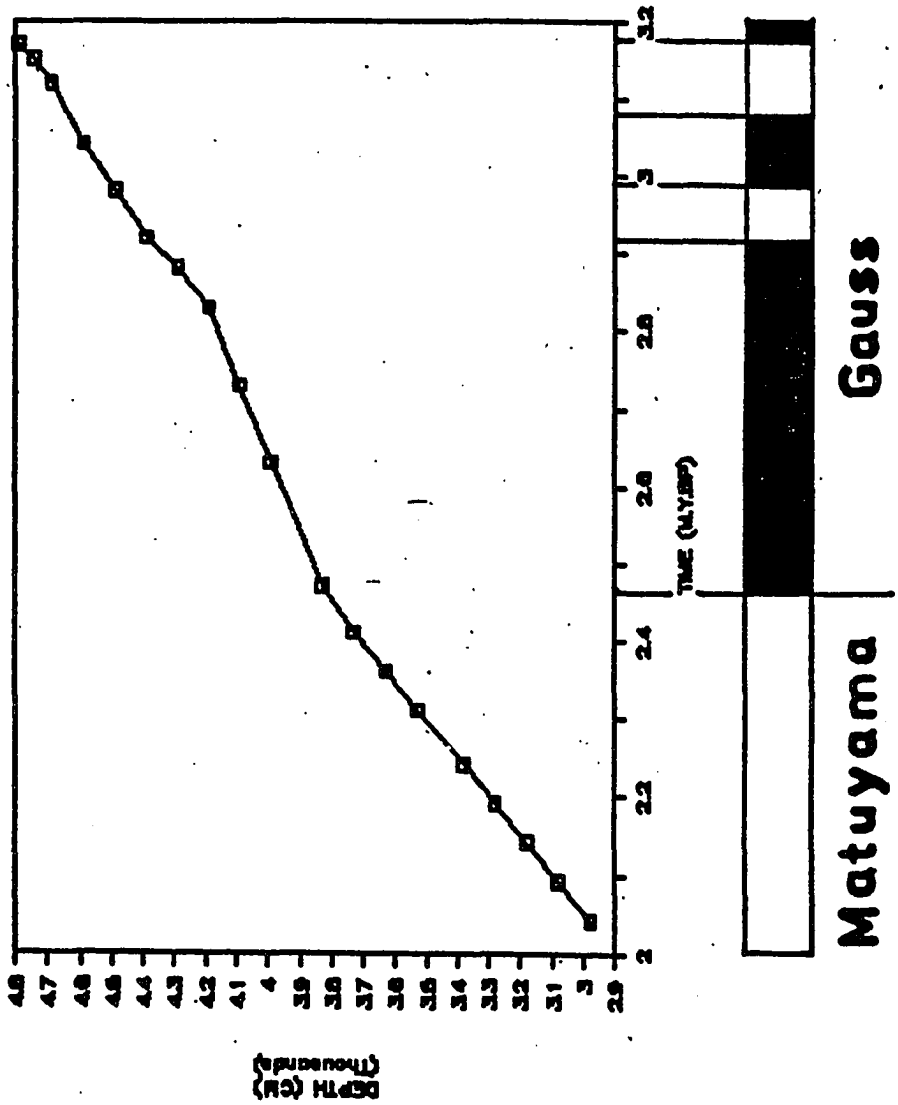


Figure 6. Depth vs. Time plot for DSDP site 572c.

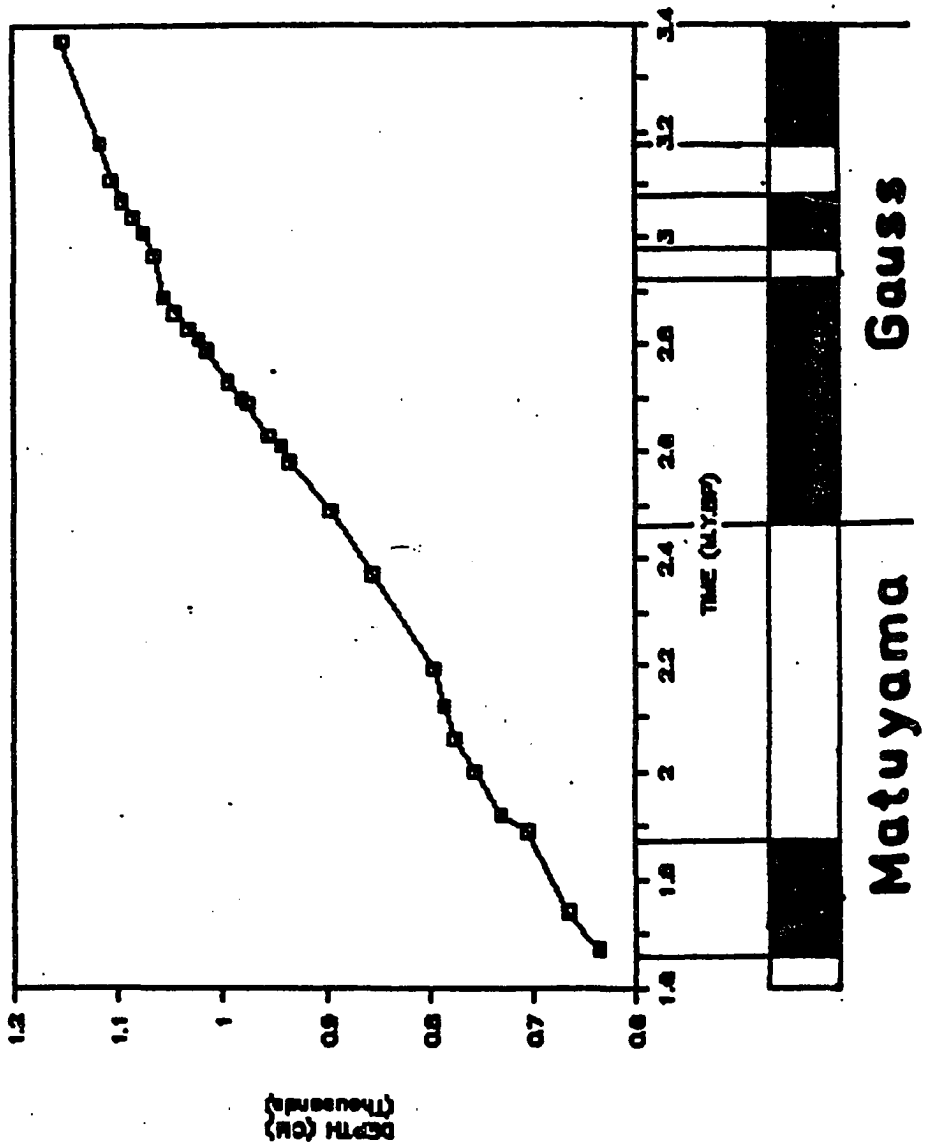


Figure 7. Depth vs. Time plot for site RC12-66.

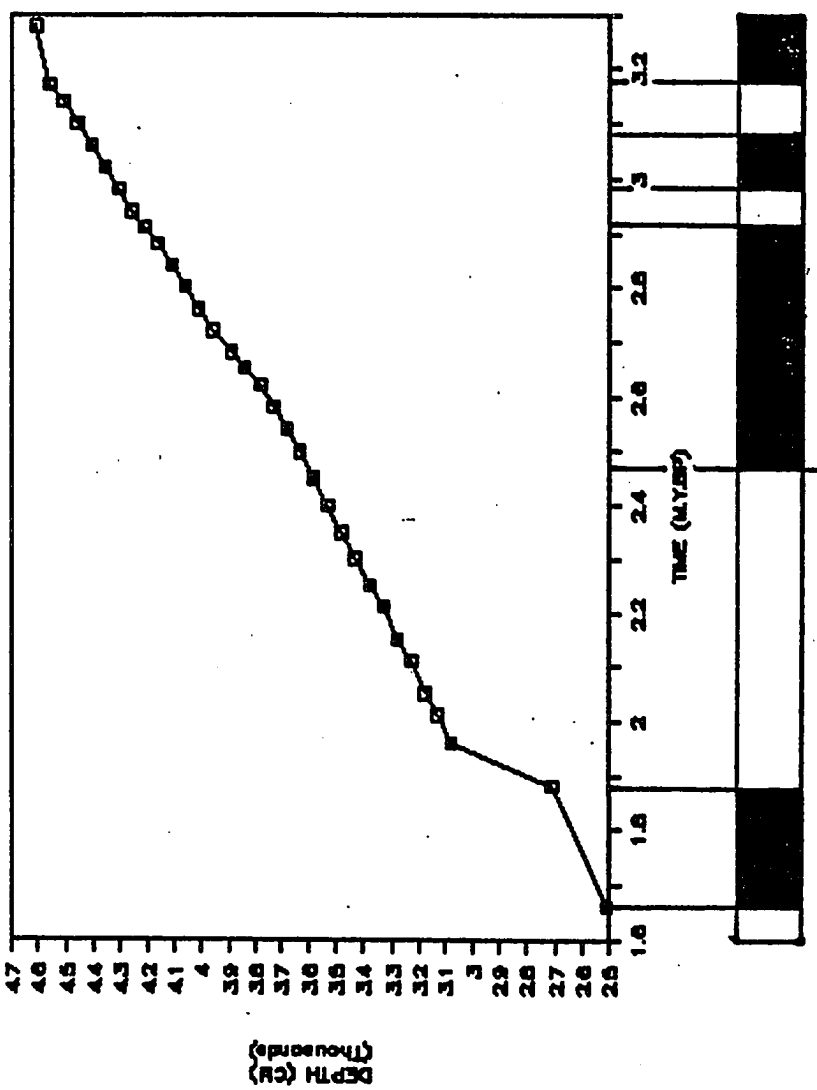


Figure 8. Depth vs. Time plot for DSDP site 573.

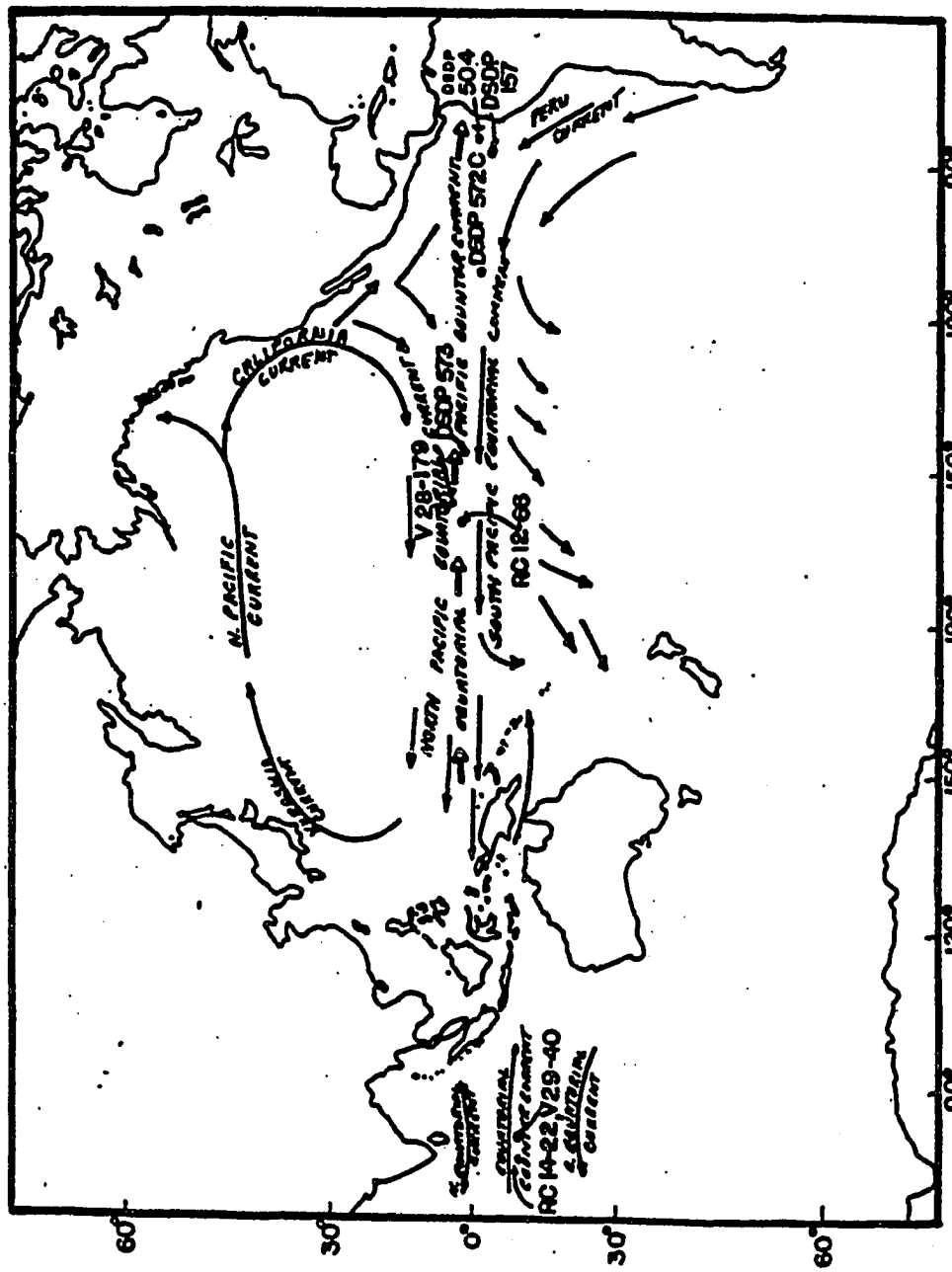


Figure 9. Location of sites sampled

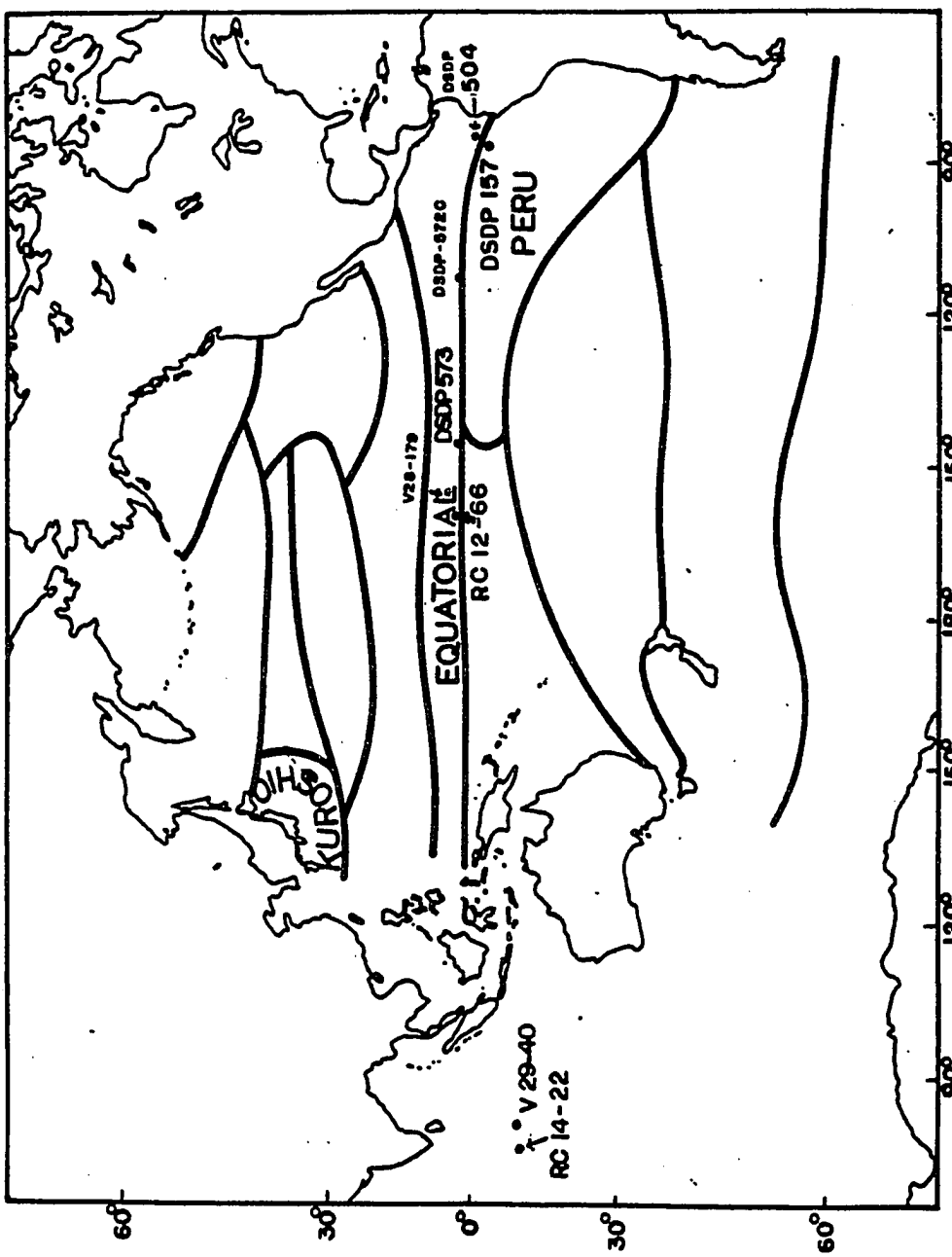


Figure 10. Location of sites sampled

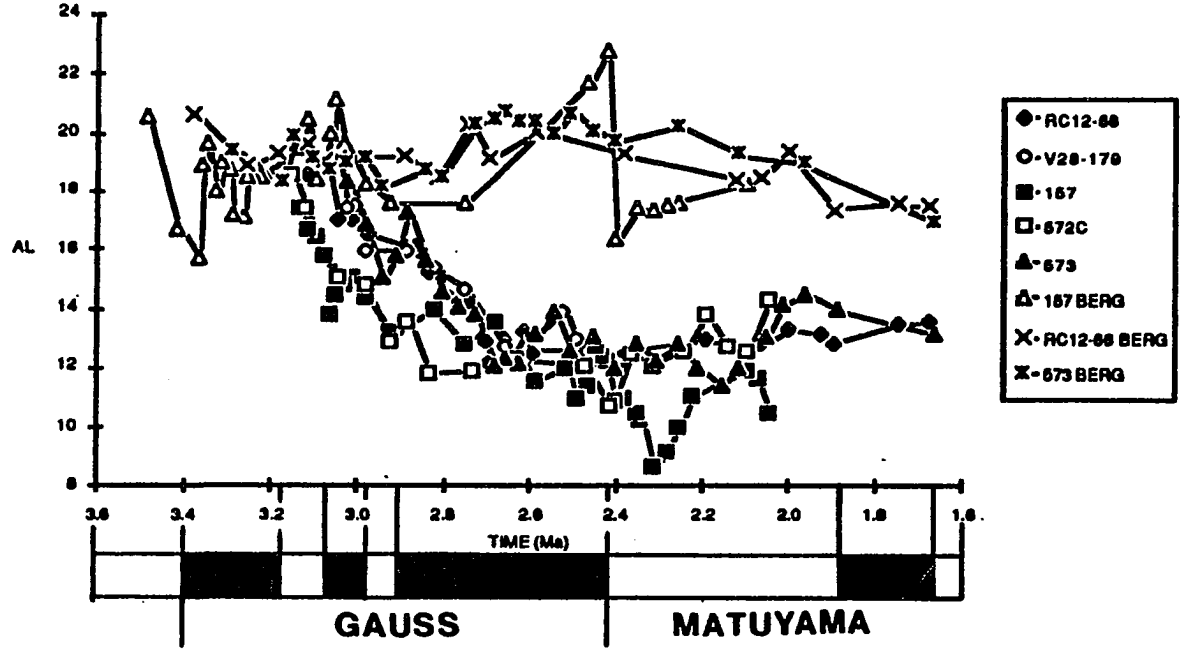


Figure 11. Change through time in mean length of the apical process in the equatorial Pacific Ocean sites.

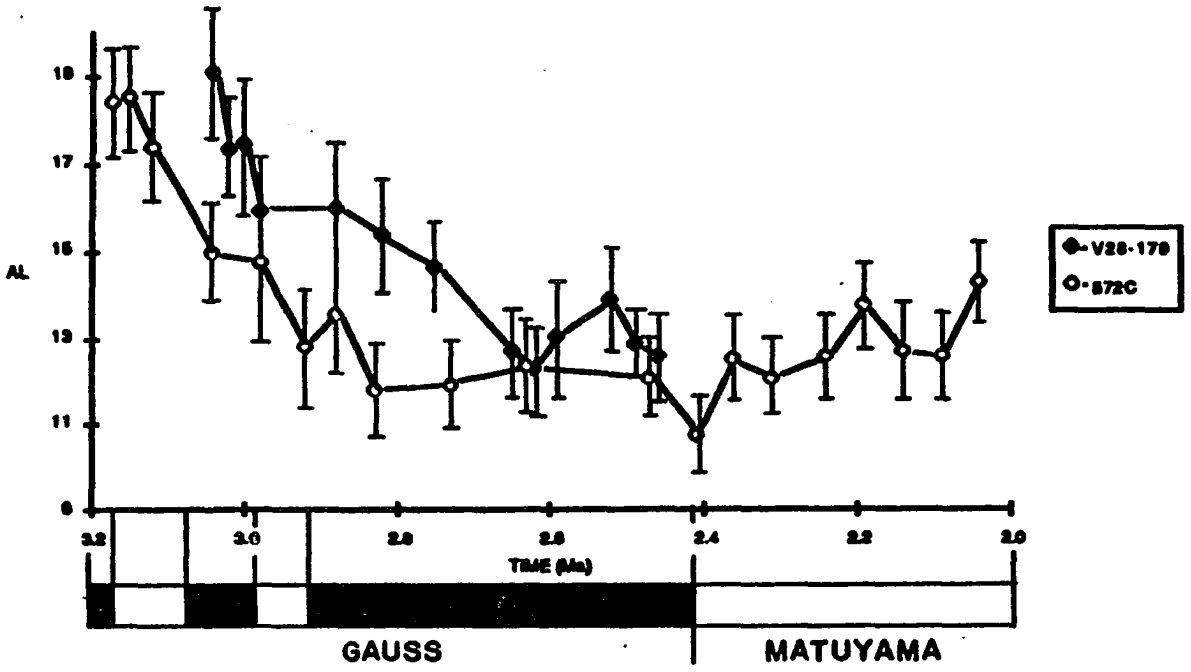


Figure 12. Change through time in mean length of the apical process in DSDP site 572c and core V28-179.

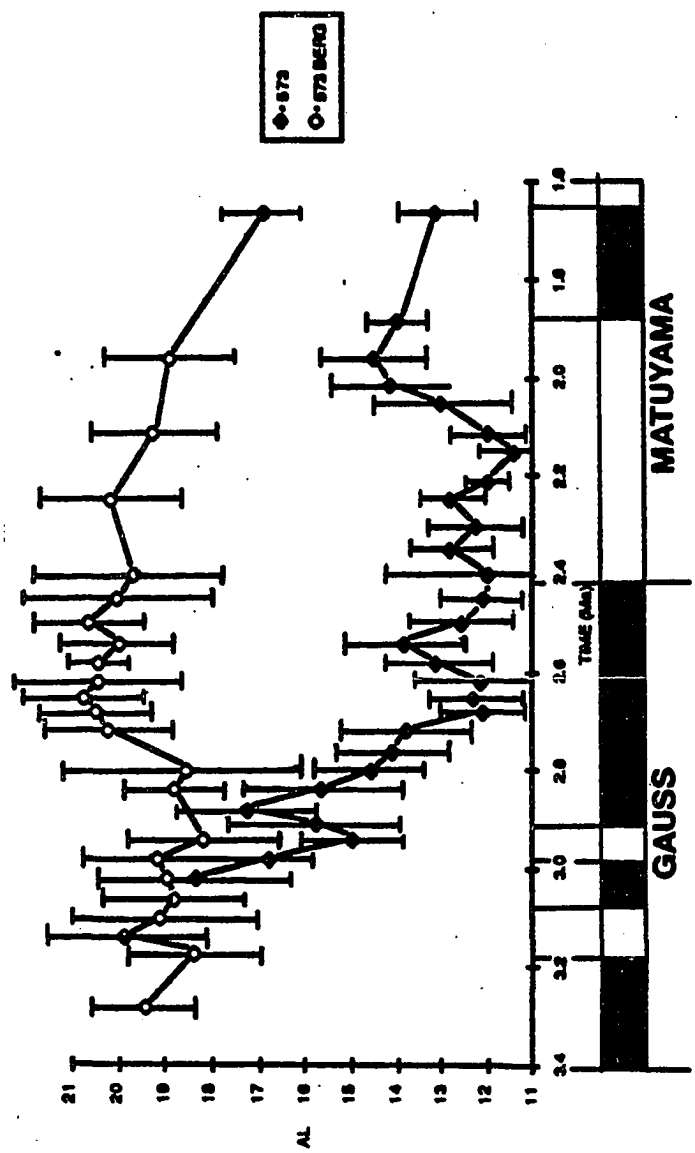


Figure 13. Change through time in mean length of the apical process in DSDP site 573.

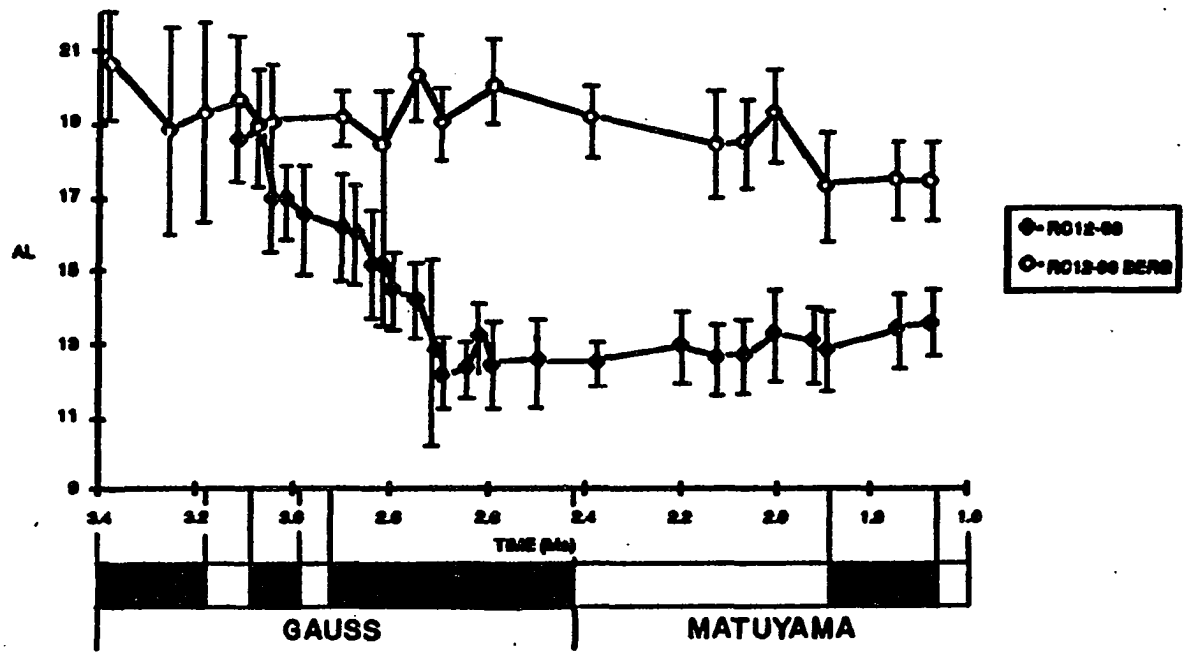


Figure 14. Change through time in mean length of the apical process in site RC12-66.

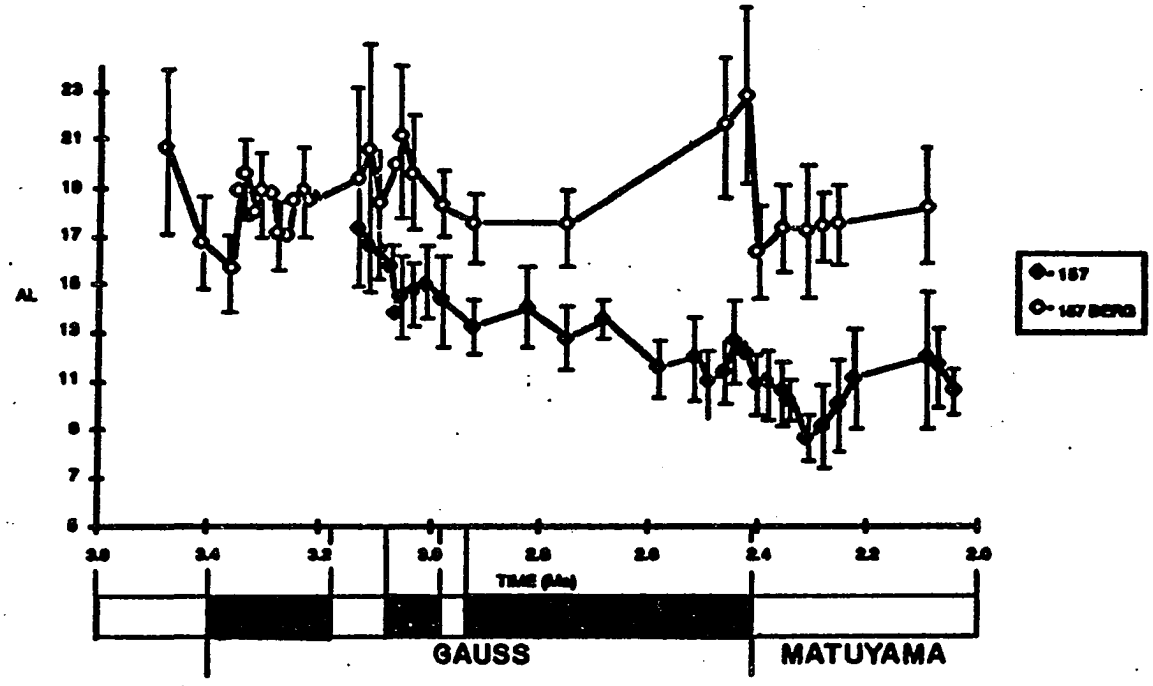


Figure 15. Change through time in mean length of the apical process in DSDP site 157.

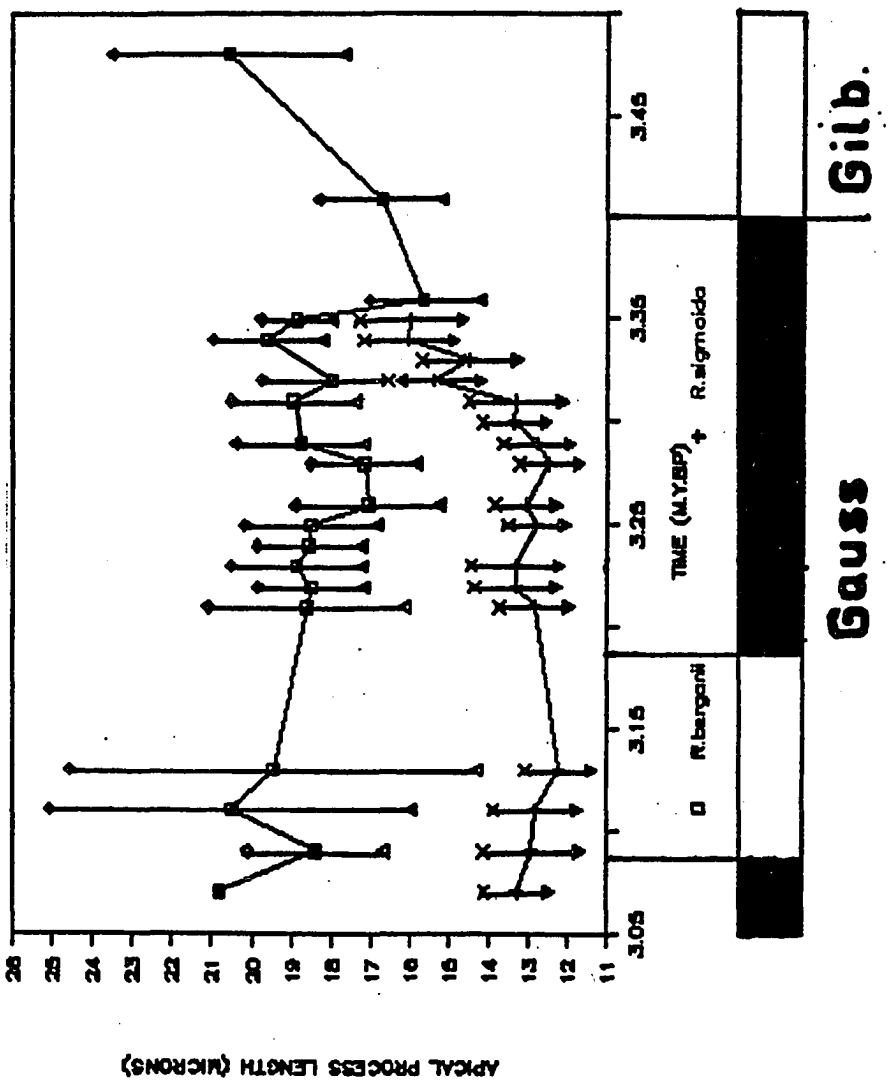


Figure 16. Change through time in mean length of the apical process in DSDP site 157.

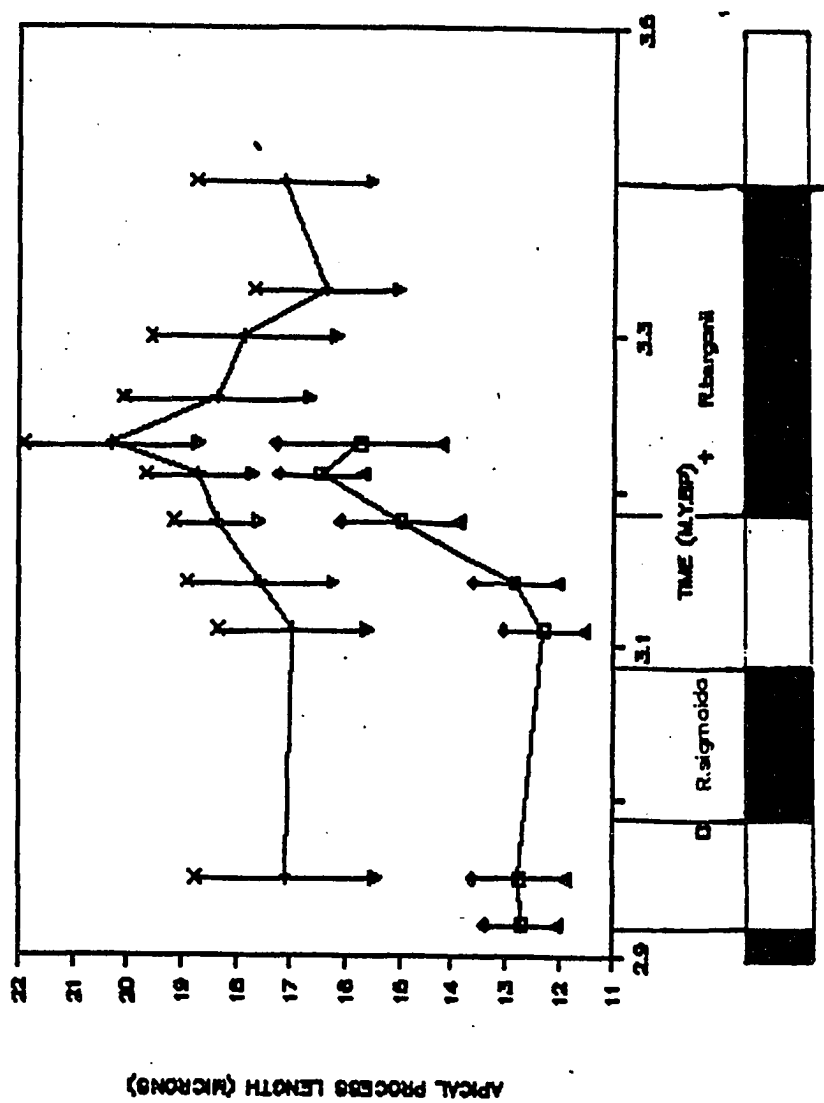


Figure 17. Change through time in mean length of the apical process in DSDP site 504.

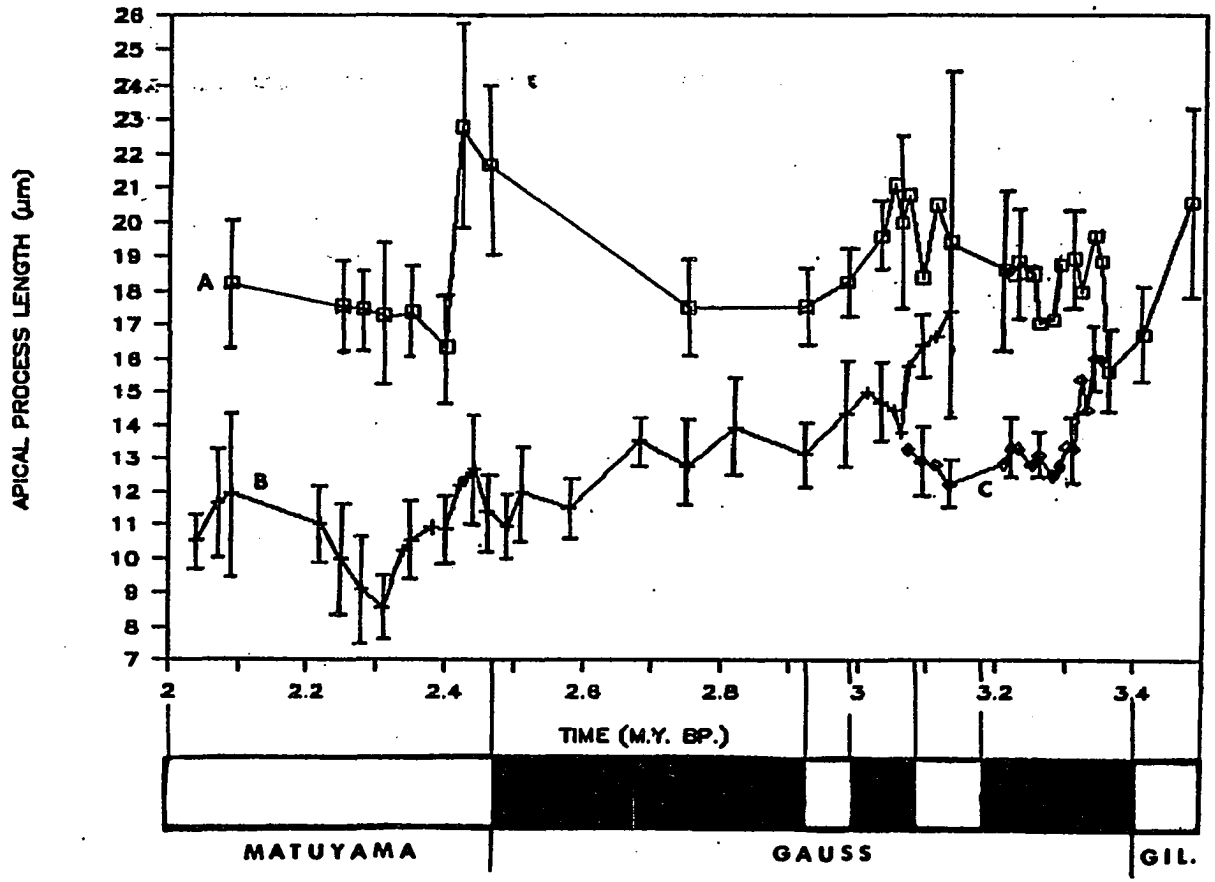


Figure 18. Change through time in mean apical process length in DSDP Site 157. A=R.bergonii, B=R.praebergonii,C=R.sigmoida

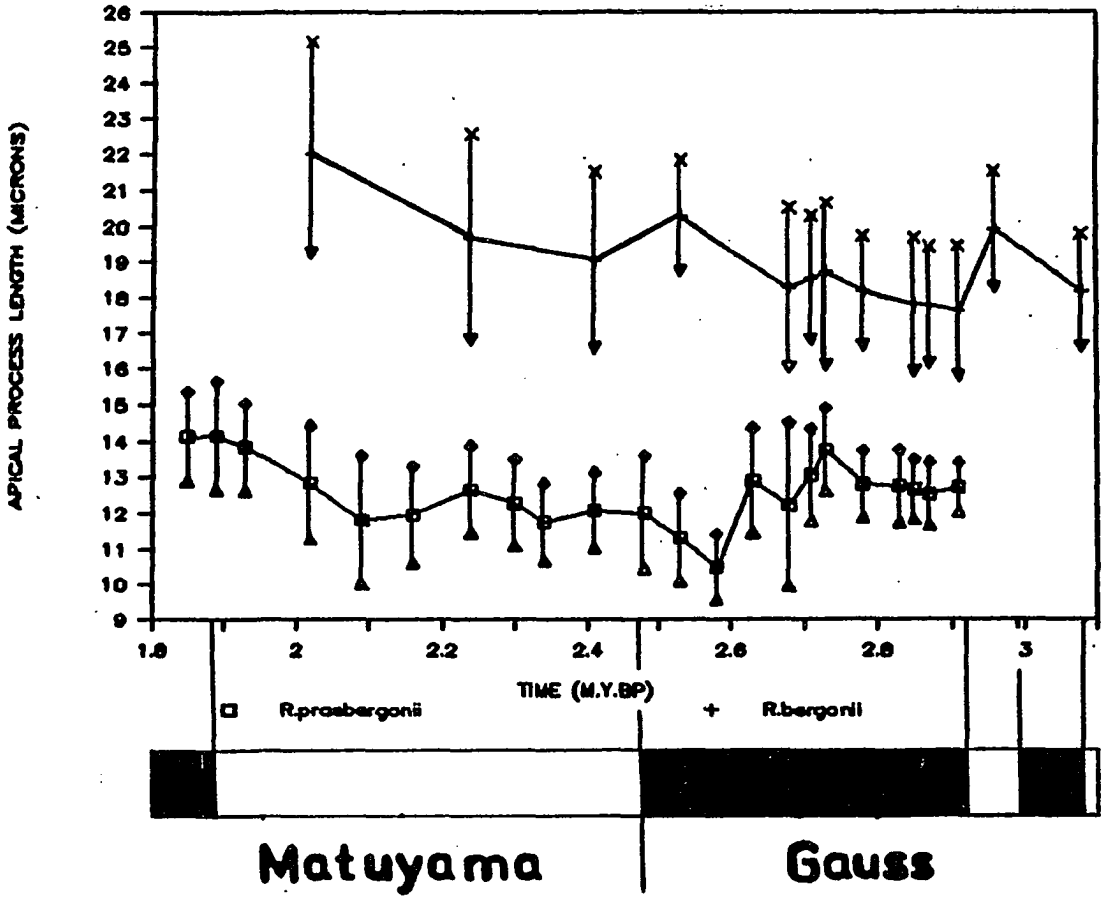


Figure 19. Change through time in mean length of the apical process in the Indian Ocean sites.

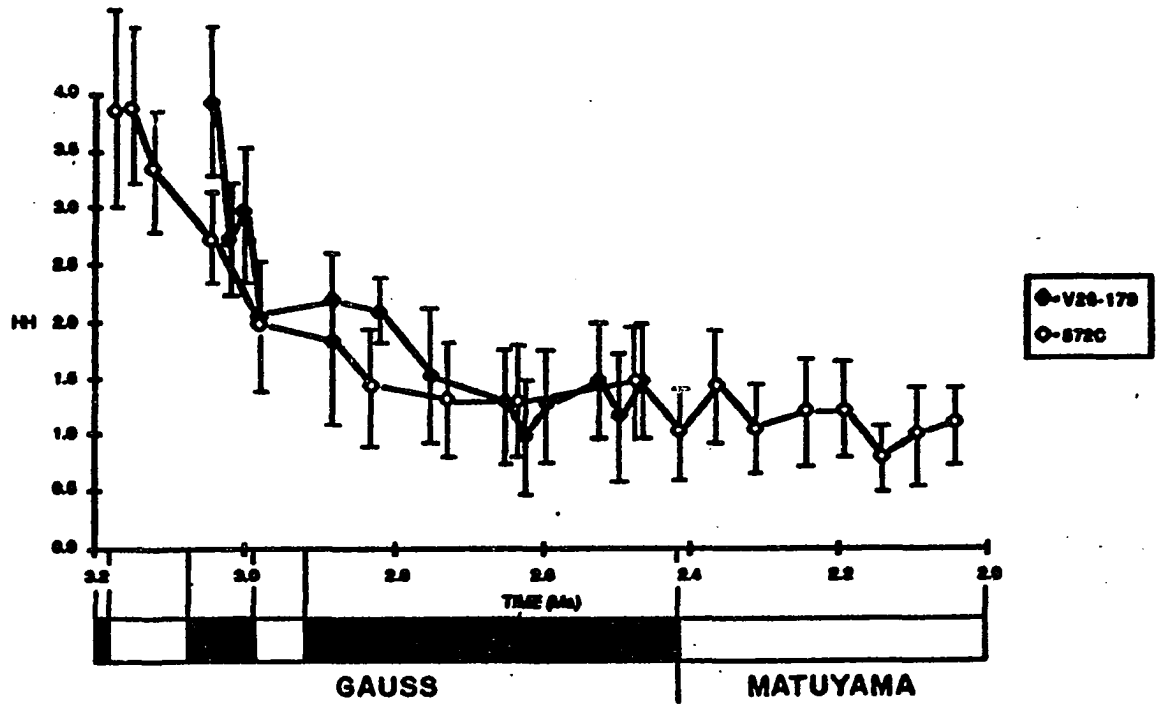


Figure 20. Change through time in mean height of the hyaline area in DSDP site 572c and core V28-179.

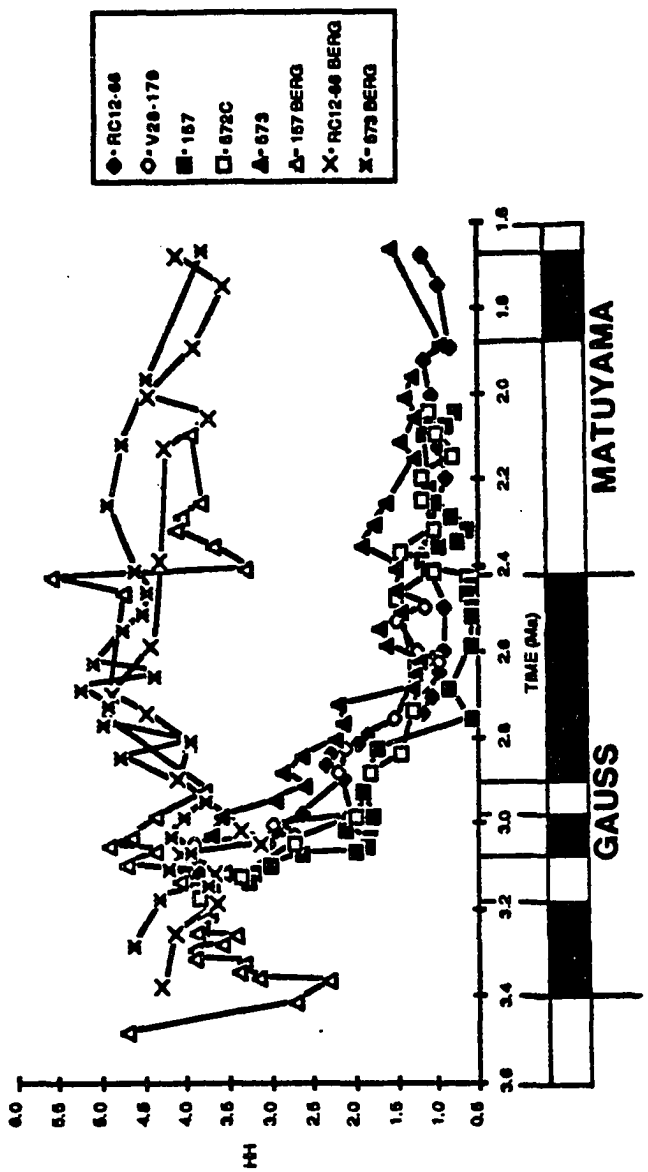


Figure 21. Change through time in mean height of the hyaline area in the equatorial Pacific Ocean sites.

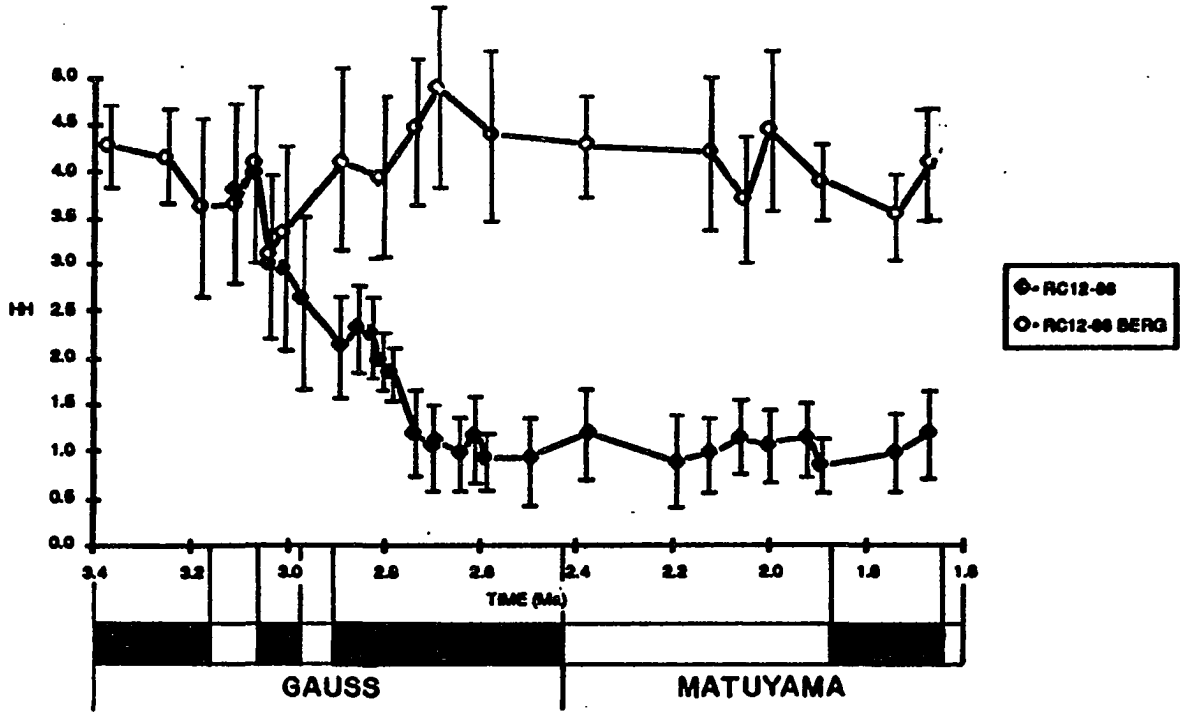


Figure 22. Change through time in mean height of the hyaline area in site RC12-66.

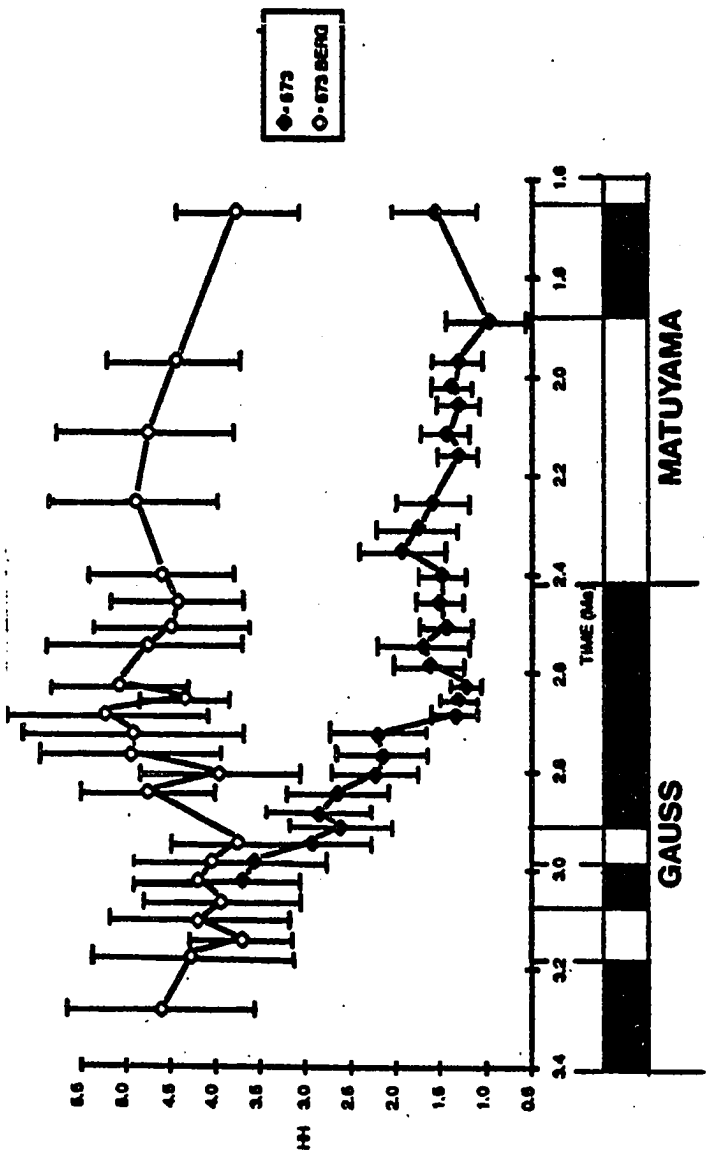


Figure 23. Change through time in mean height of the hyaline area in DSDP site 573.

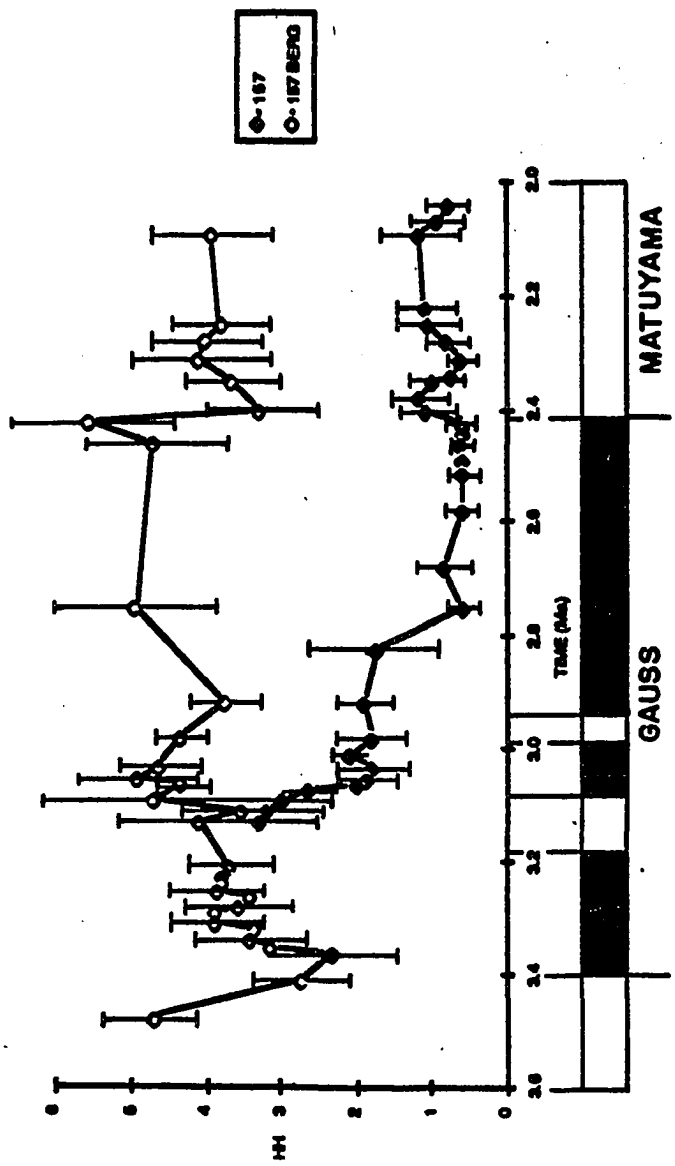


Figure 24. Change through time in mean height of the hyaline area in DSDP site 157.

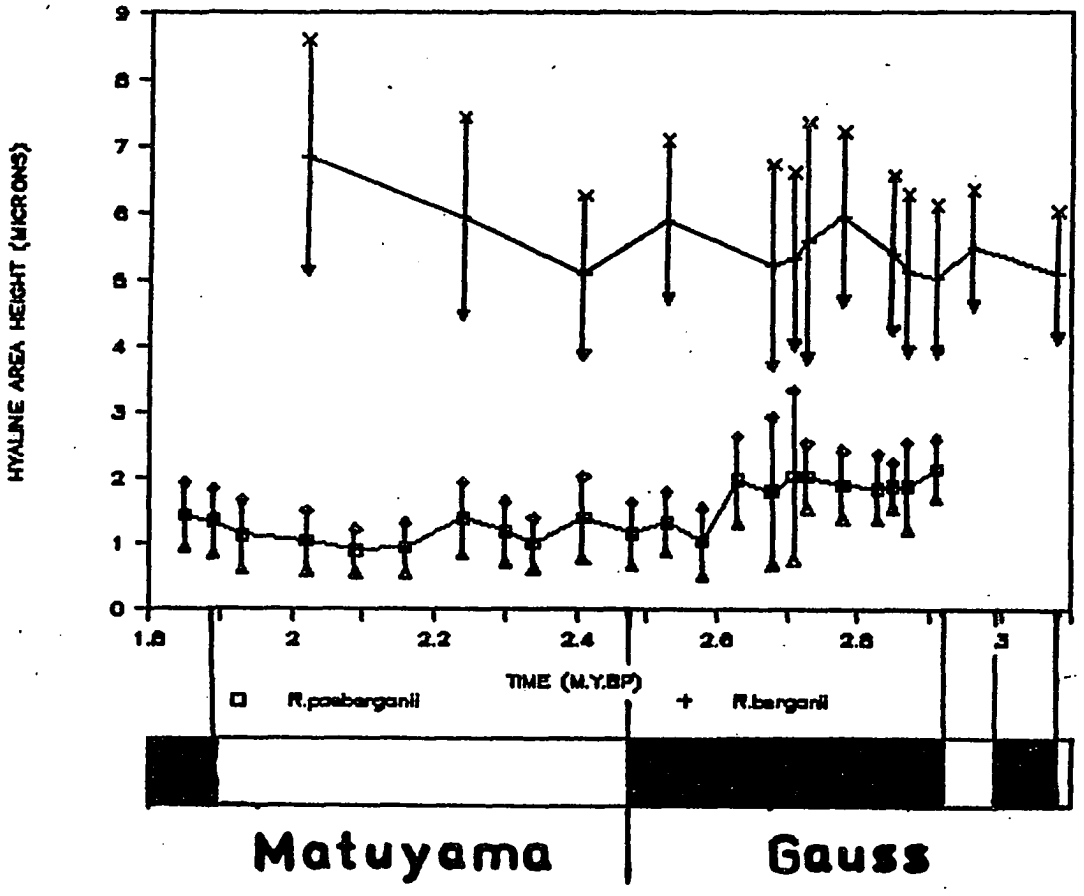


Figure 25. Change through time in mean height of the hyaline area in the Indian Ocean sites.

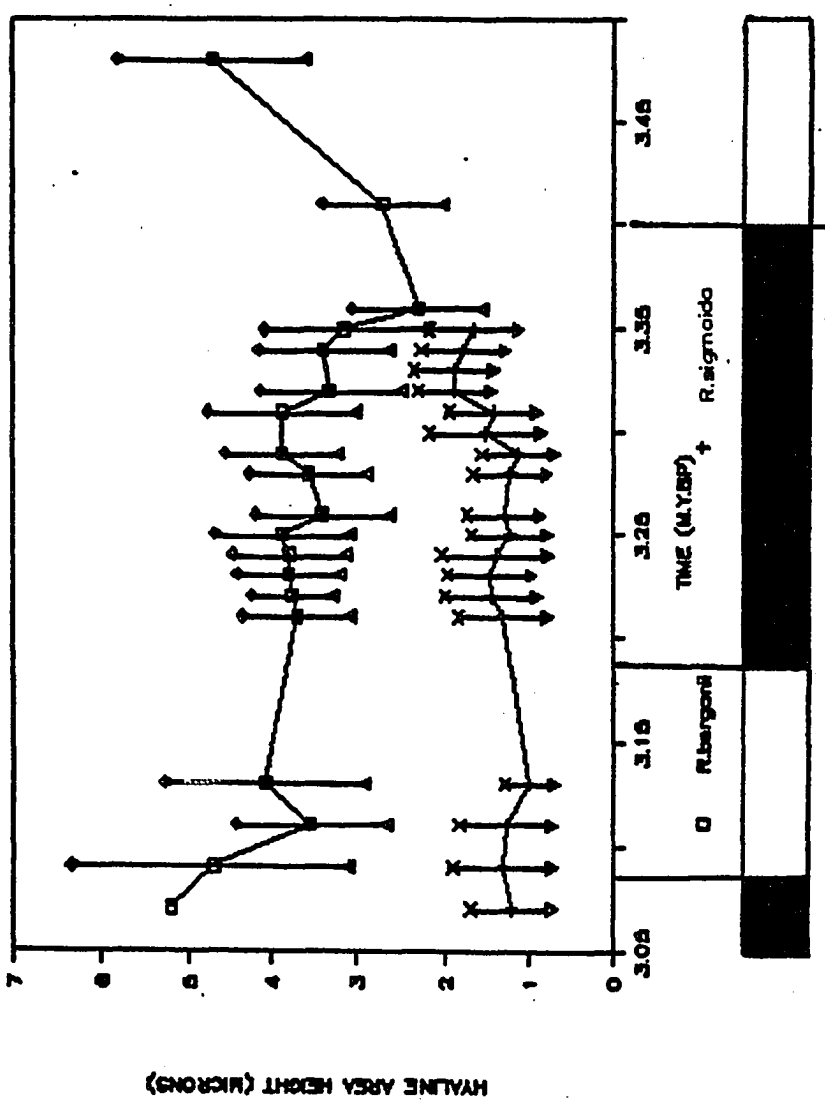


Figure 26. Change through time in mean height of the hyaline area in DSDP site 157.

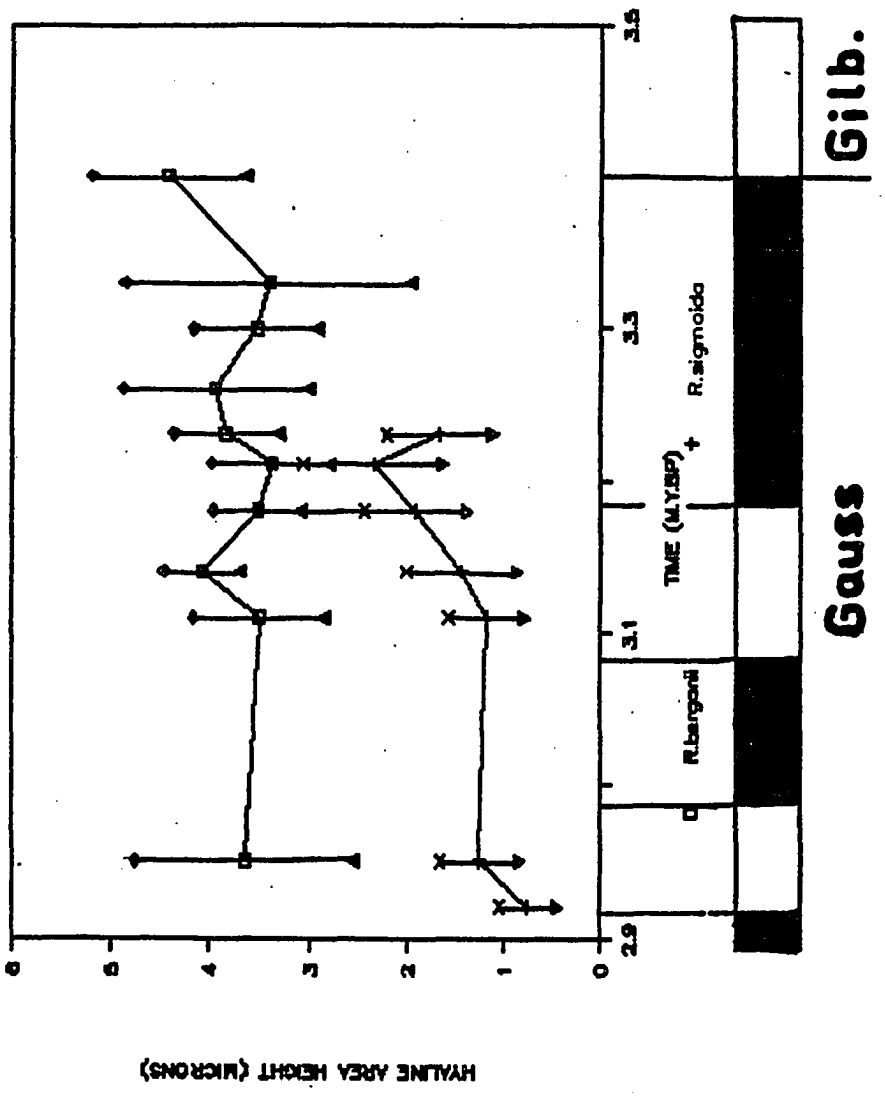


Figure 27. Change through time in mean height of the hyaline area in DSDP site 504.

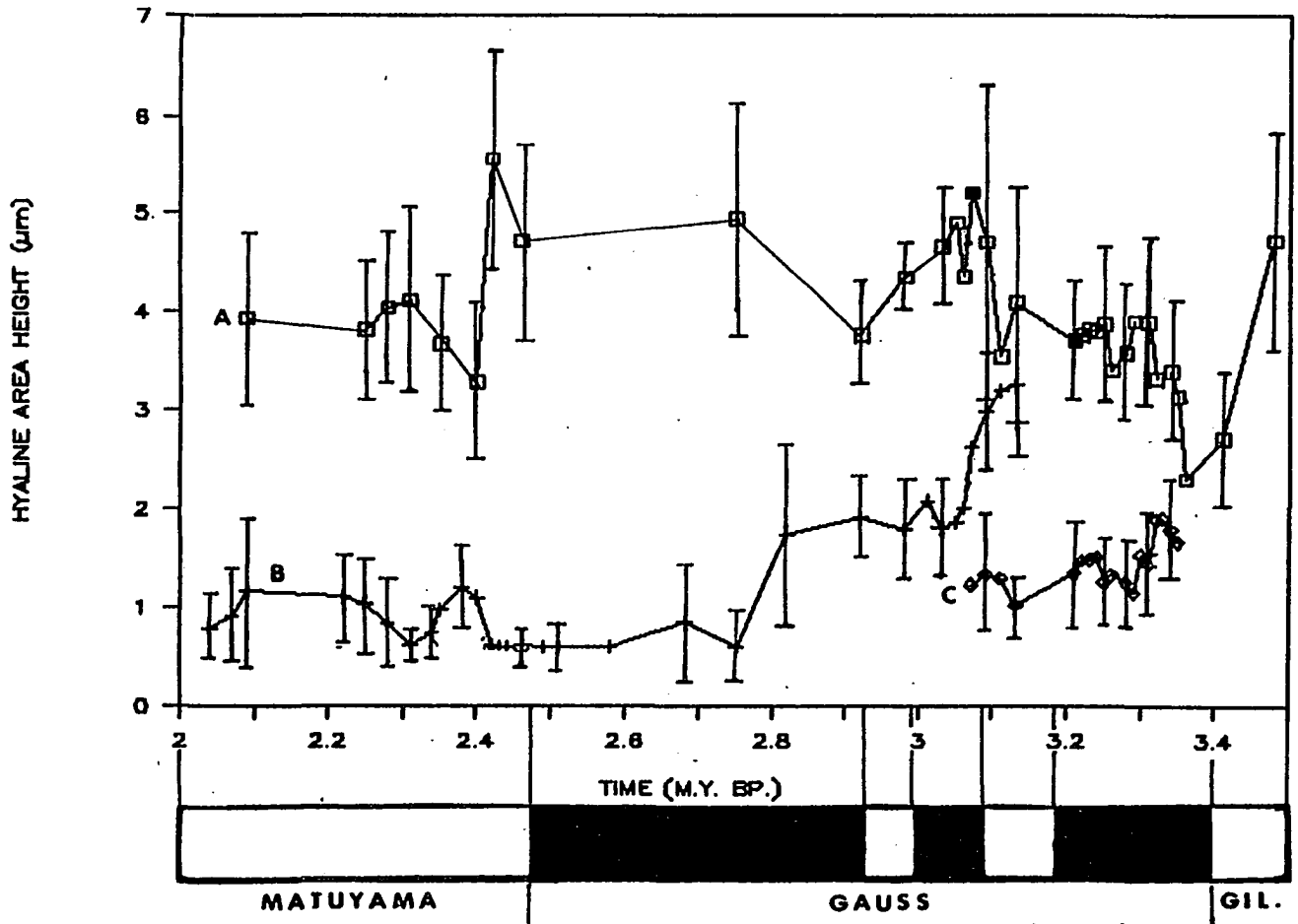


Figure 28. Change through time in mean hyaline area height in DSDP SITE 157. A=R.bergonii,B=R.praebergonii, c=R.sigmoida

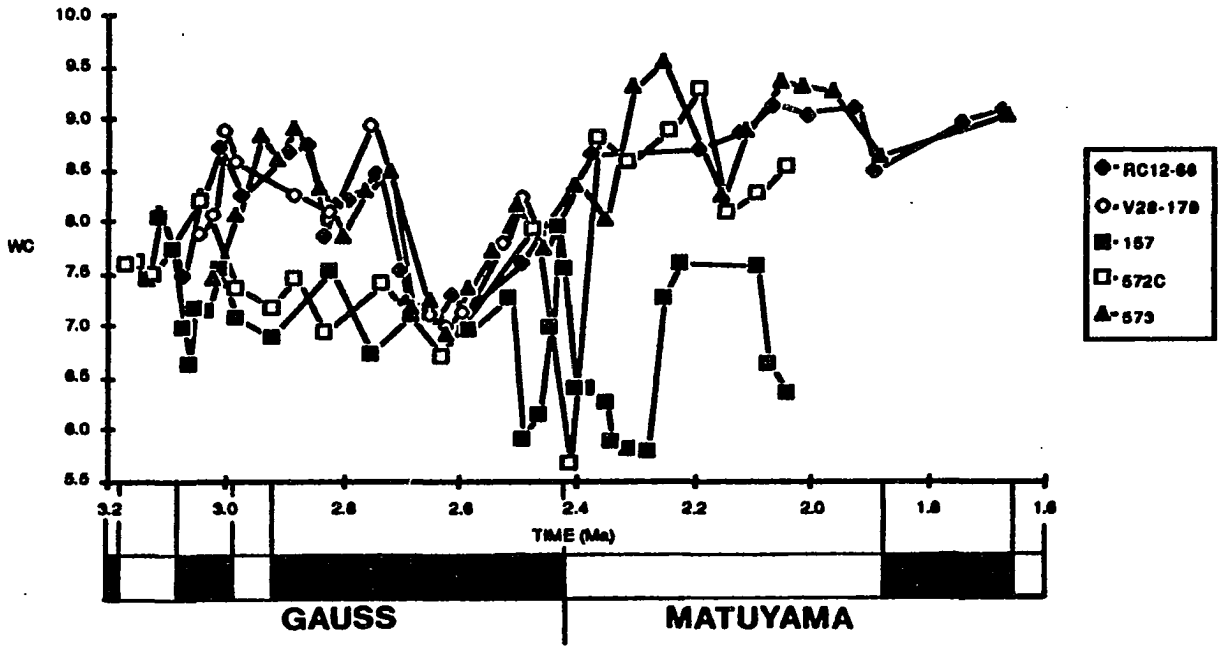


Figure 29. Change through time in mean width of the valve in the equatorial Pacific Ocean sites.

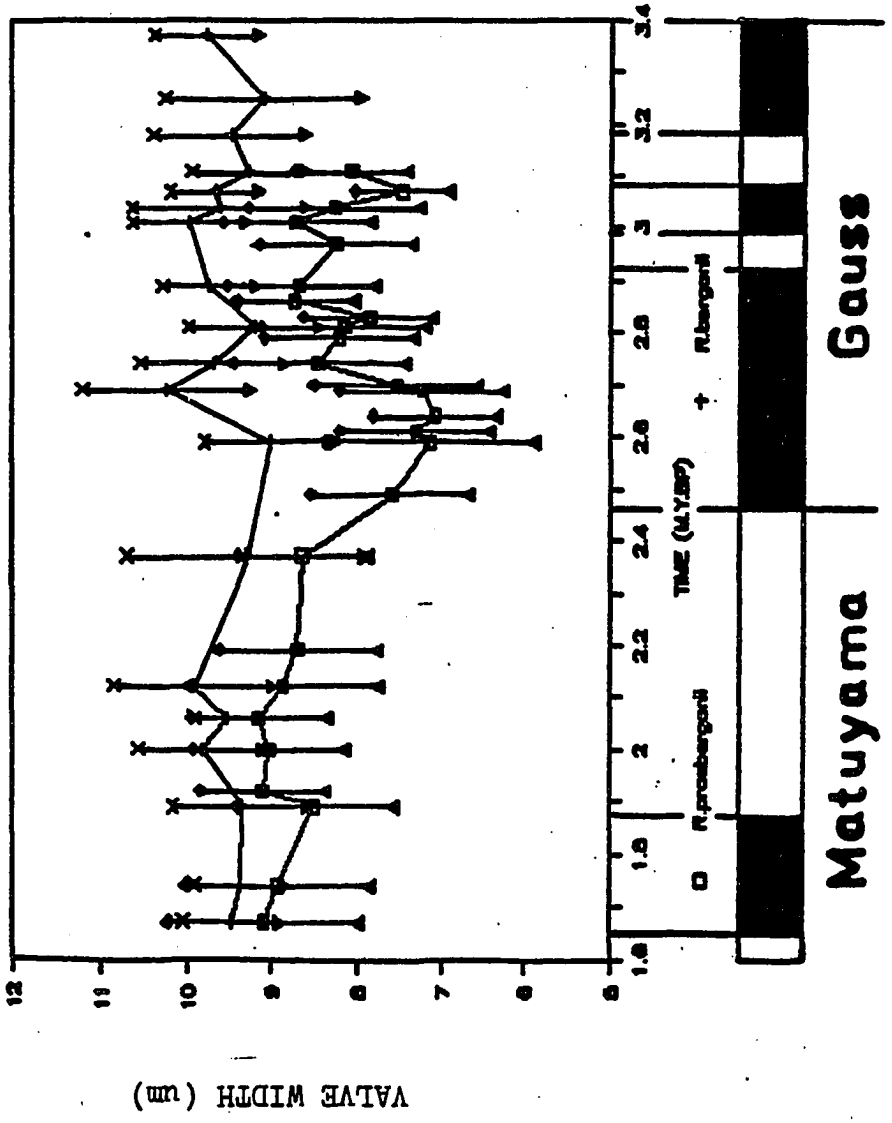


Figure 30. Change through time in mean width of the valve in site RC12-66.

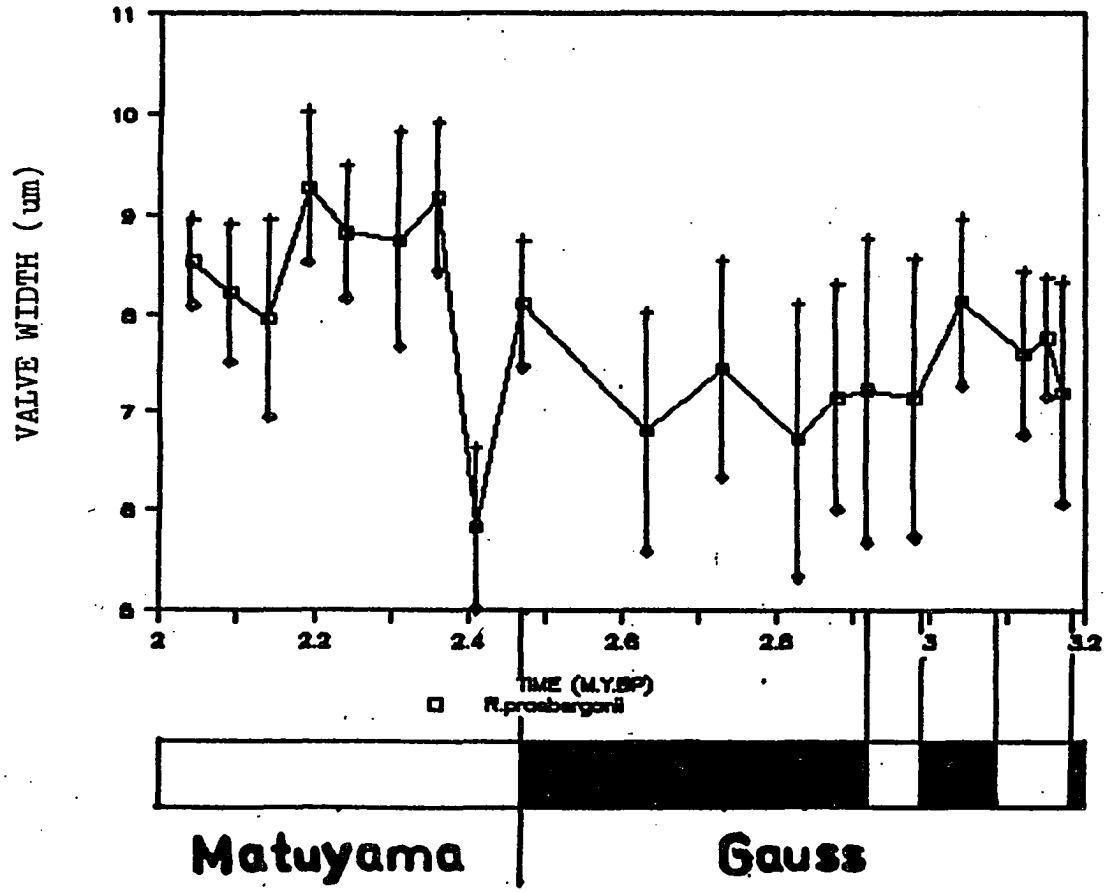


Figure 31. Change through time in mean width of the Valve in DSDP site 572c.

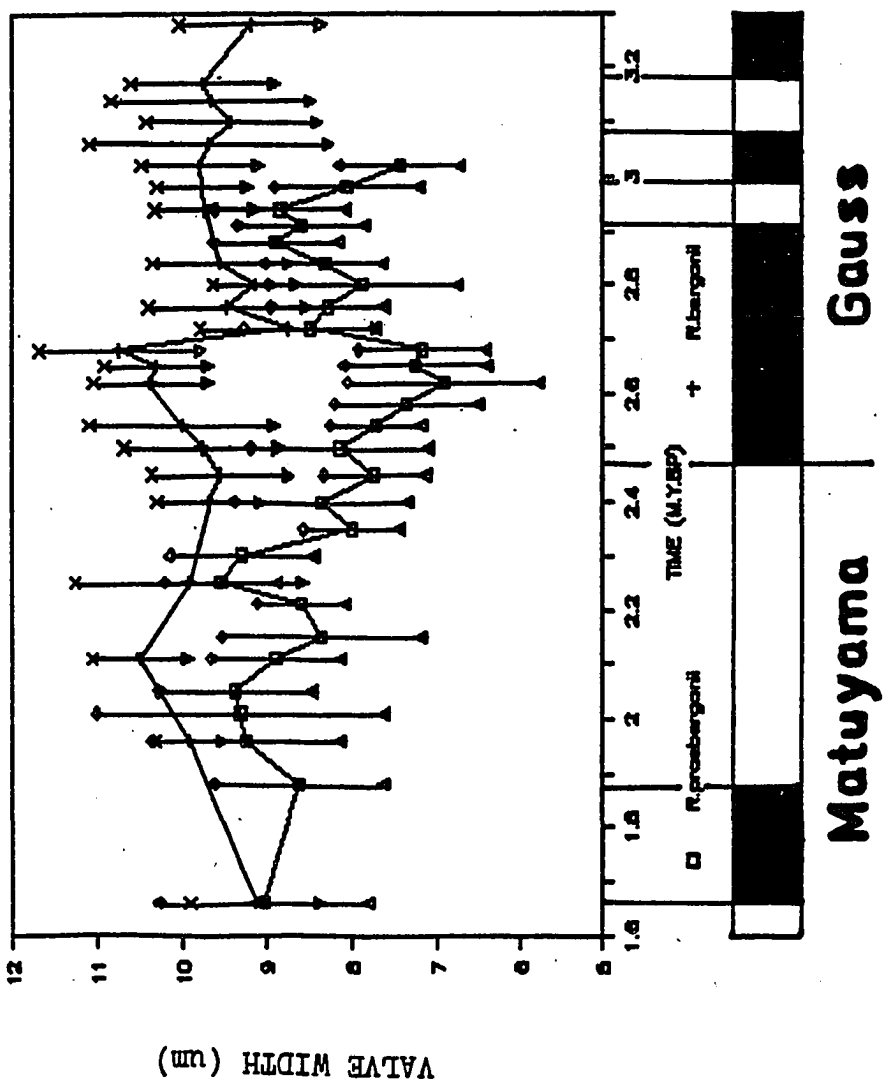


Figure 32. Change through time in mean width of the valve in DSDP site 573.

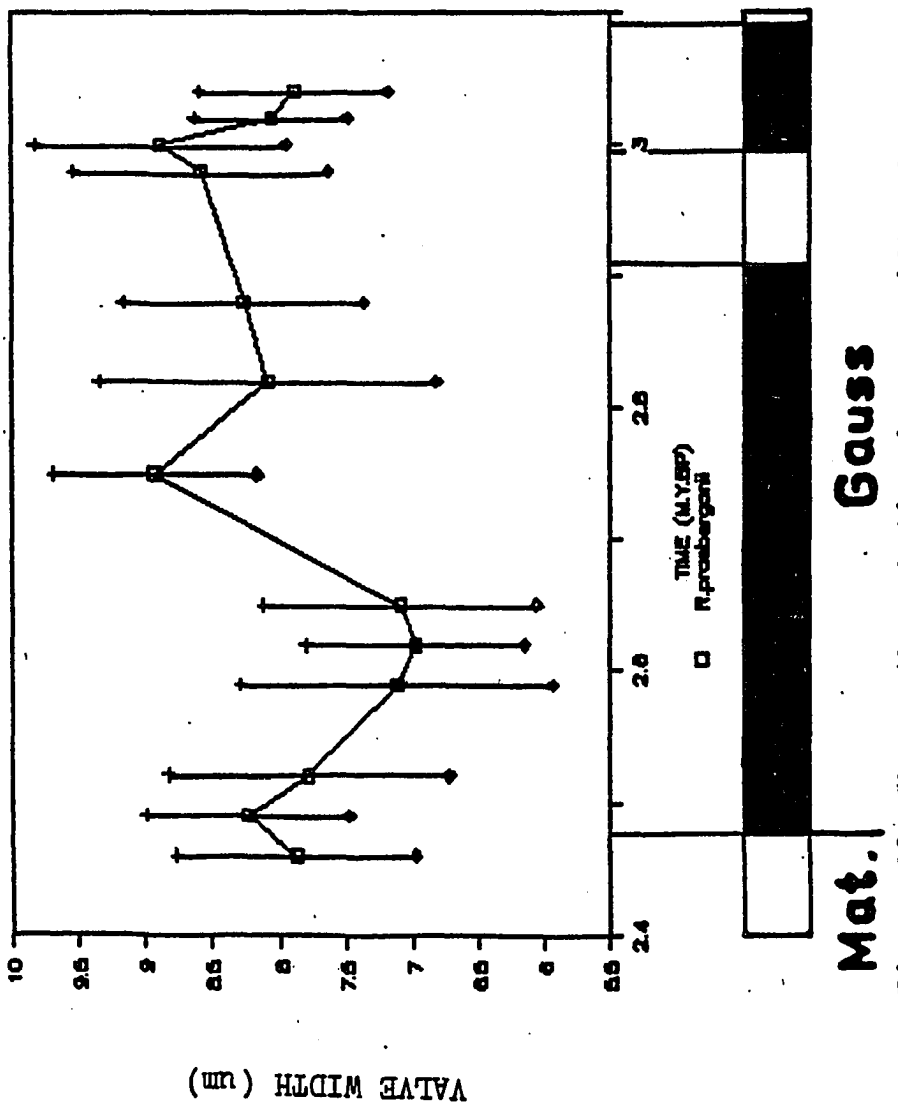


Figure 33. Change through time in mean width of the valve in site V28-179.

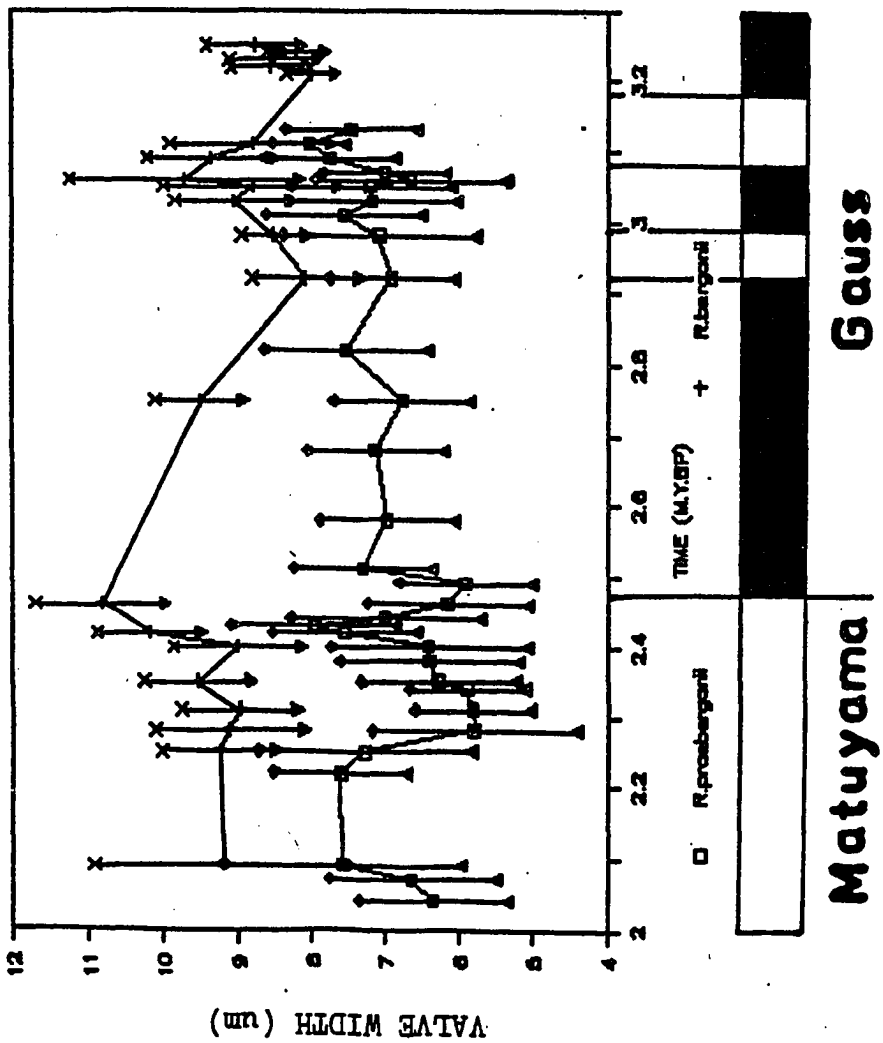


Figure 34. Change through time in mean width of the valve in DSDP site 157.

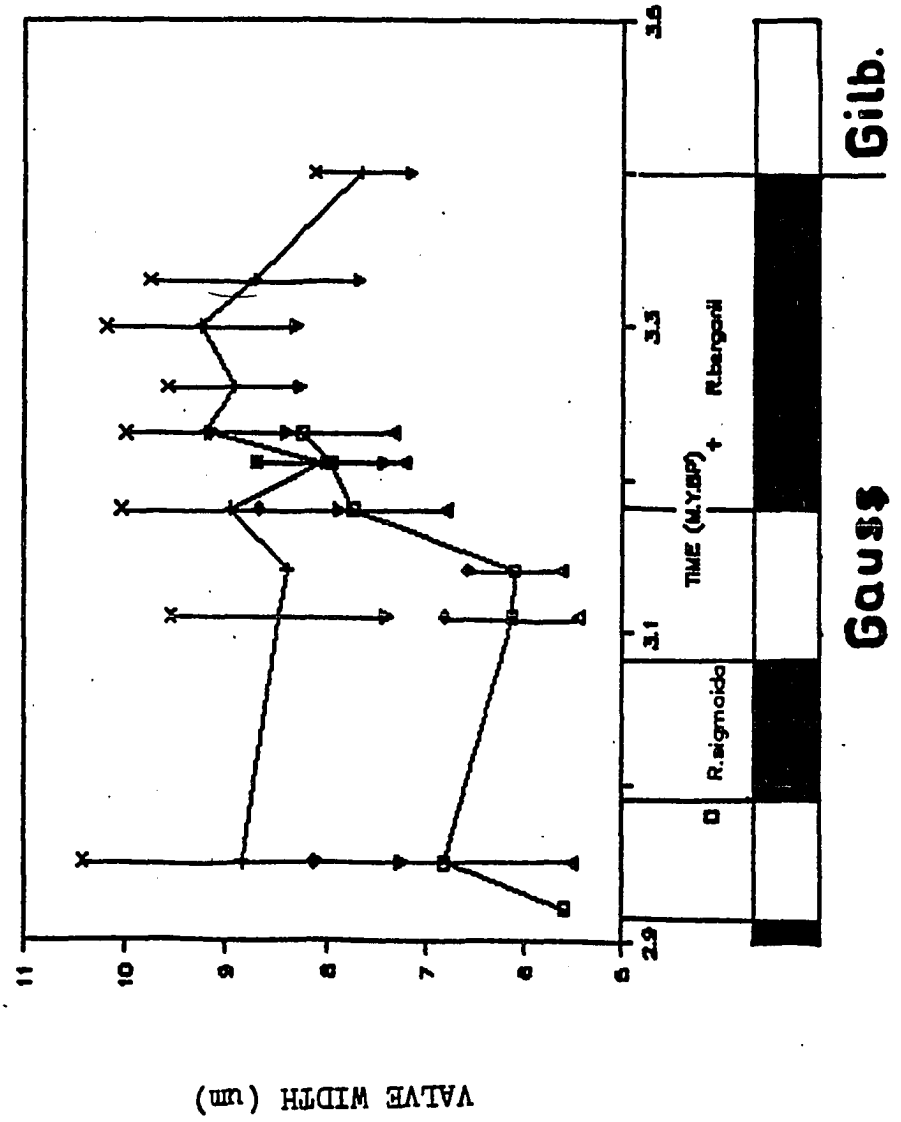


Figure 35. Change through time in mean width of the valve in DSDP site 504.

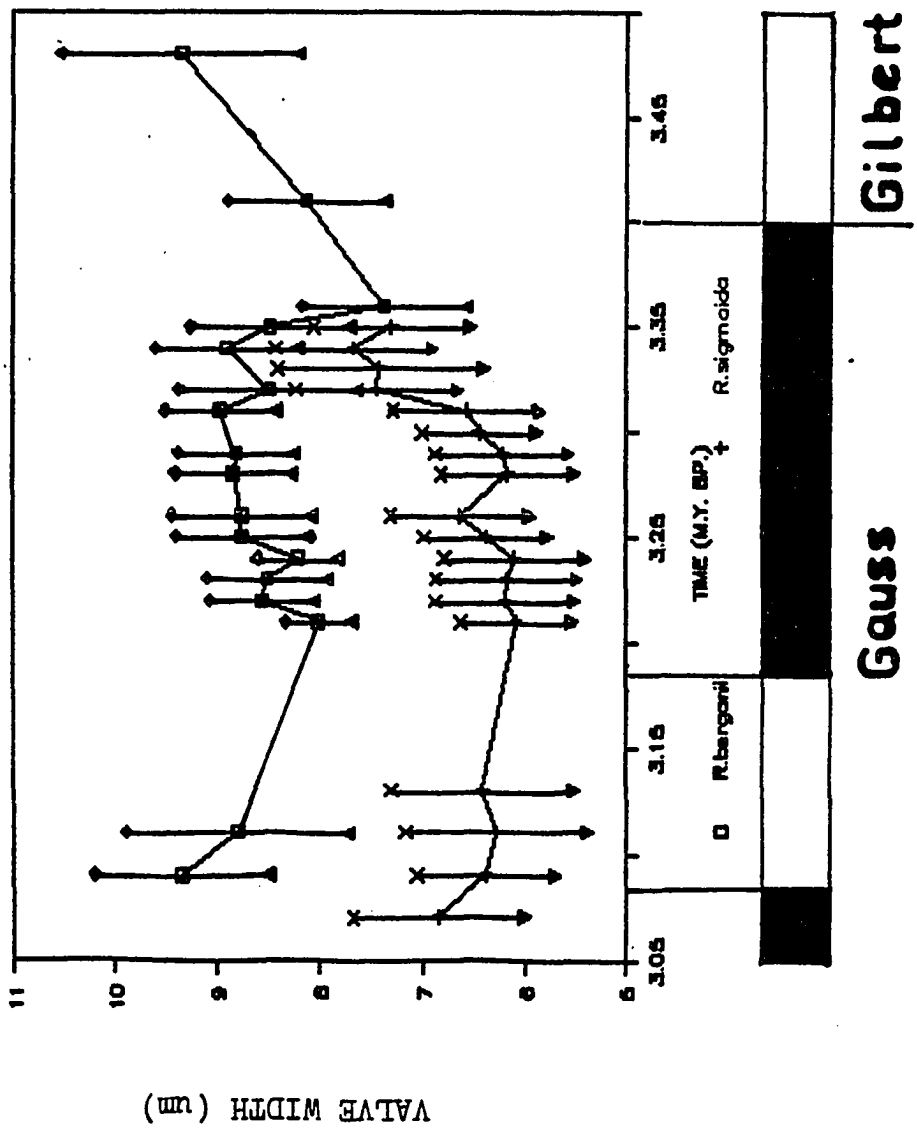


Figure 36. Change through time in mean width of the valve in DSDP site 157.

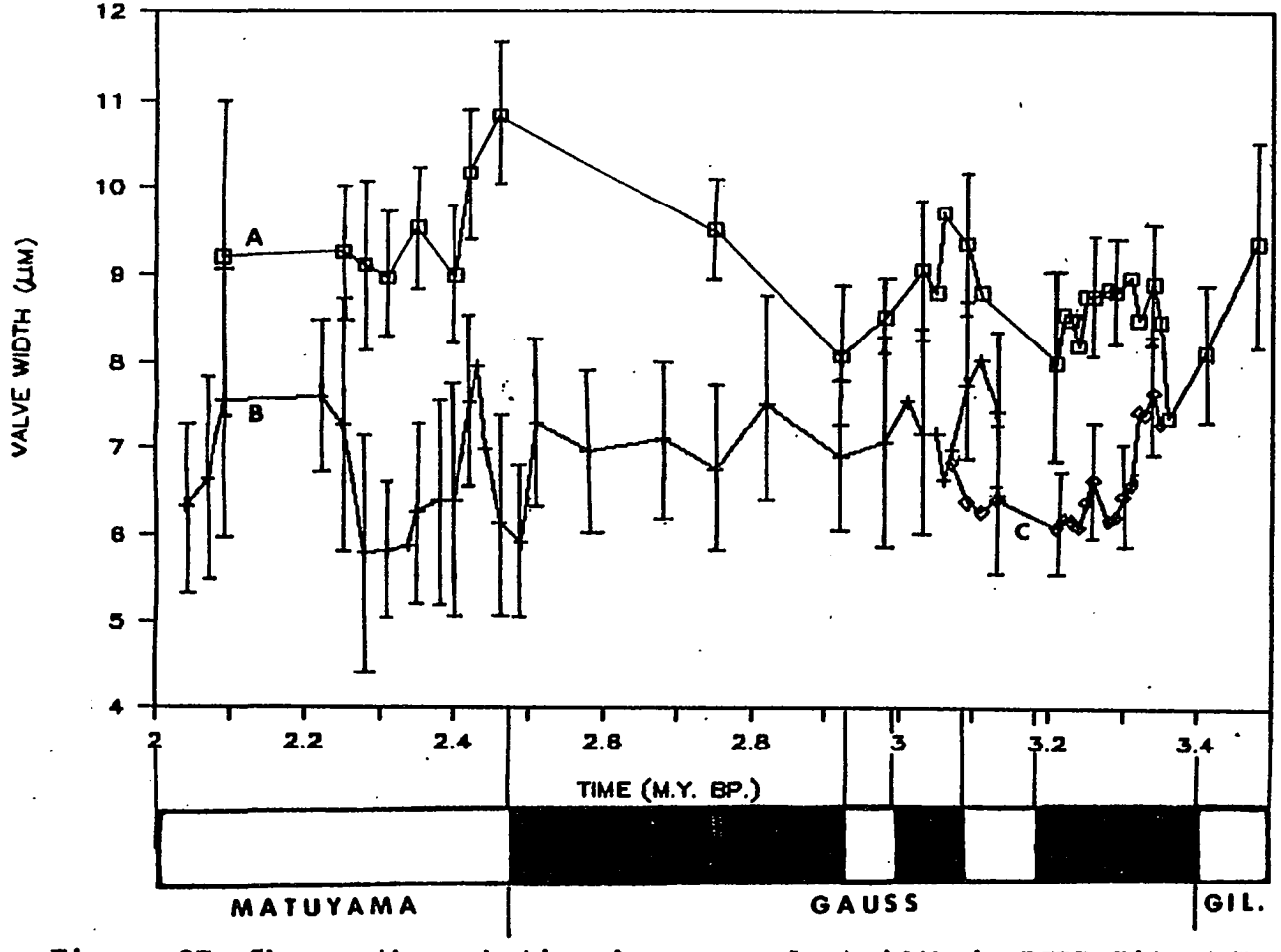


Figure 37. Change through time in mean valve width in DSDP Site 157. A=R.bergonii, B= R.praebergonii, c= R.sigmoida

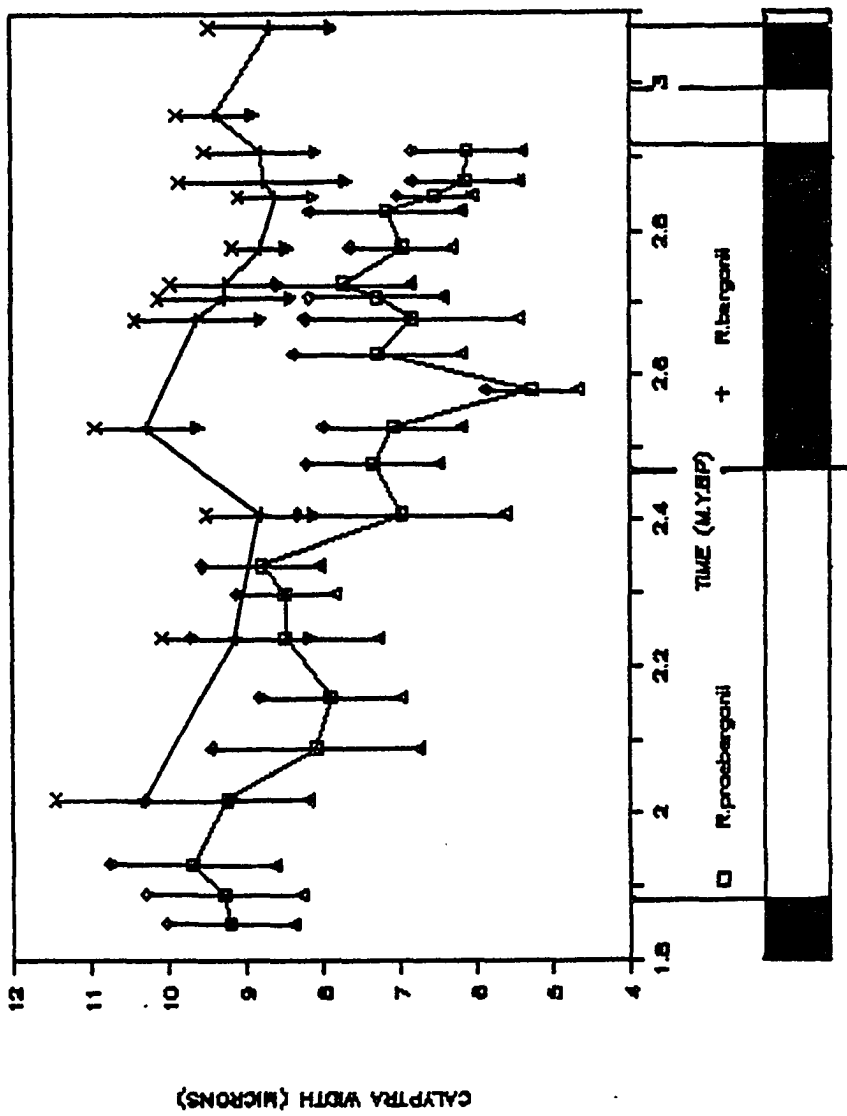


Figure 38. Change through time in mean width of the valve in site V29-40.

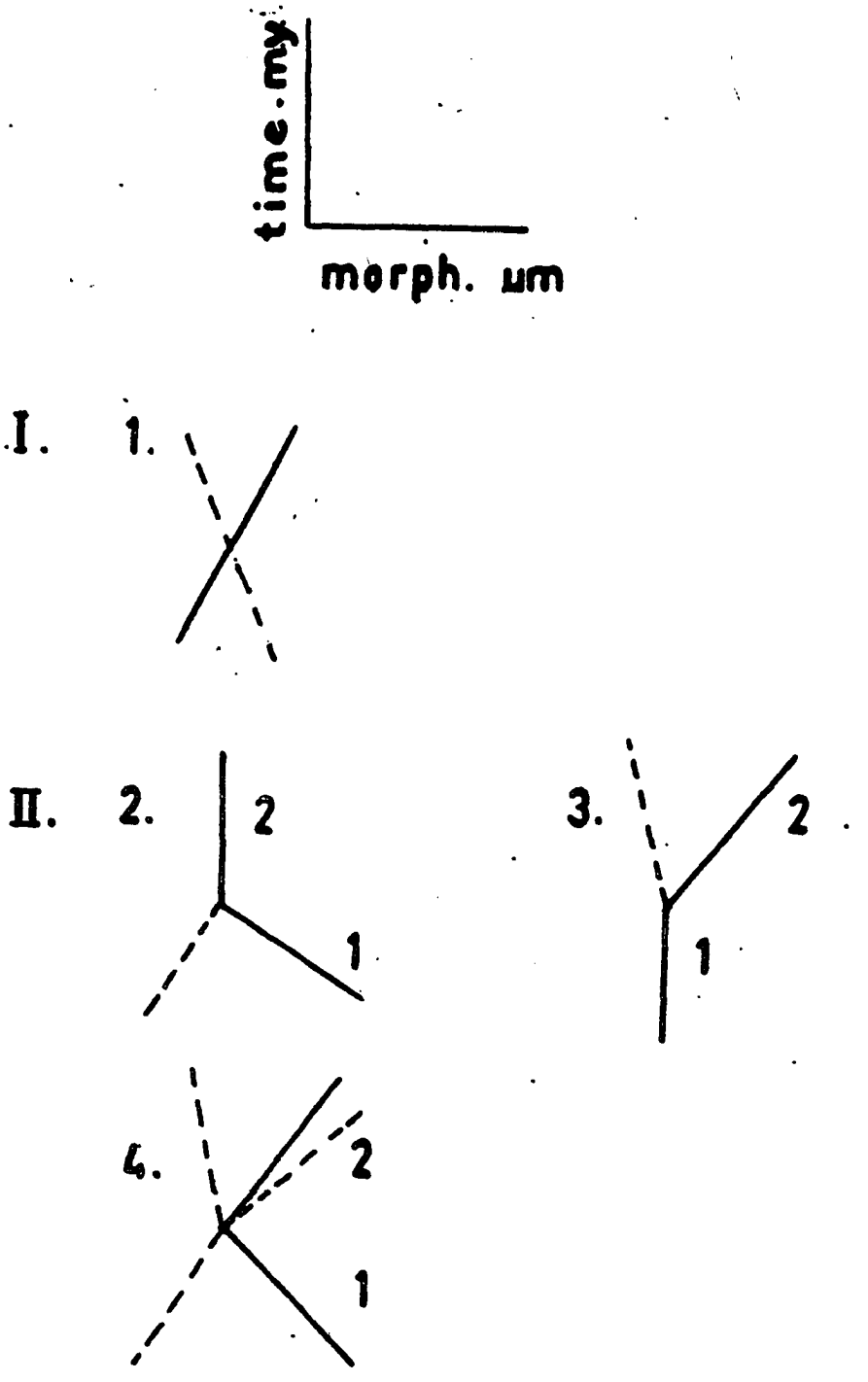


Figure 39. Hierarchical linear models

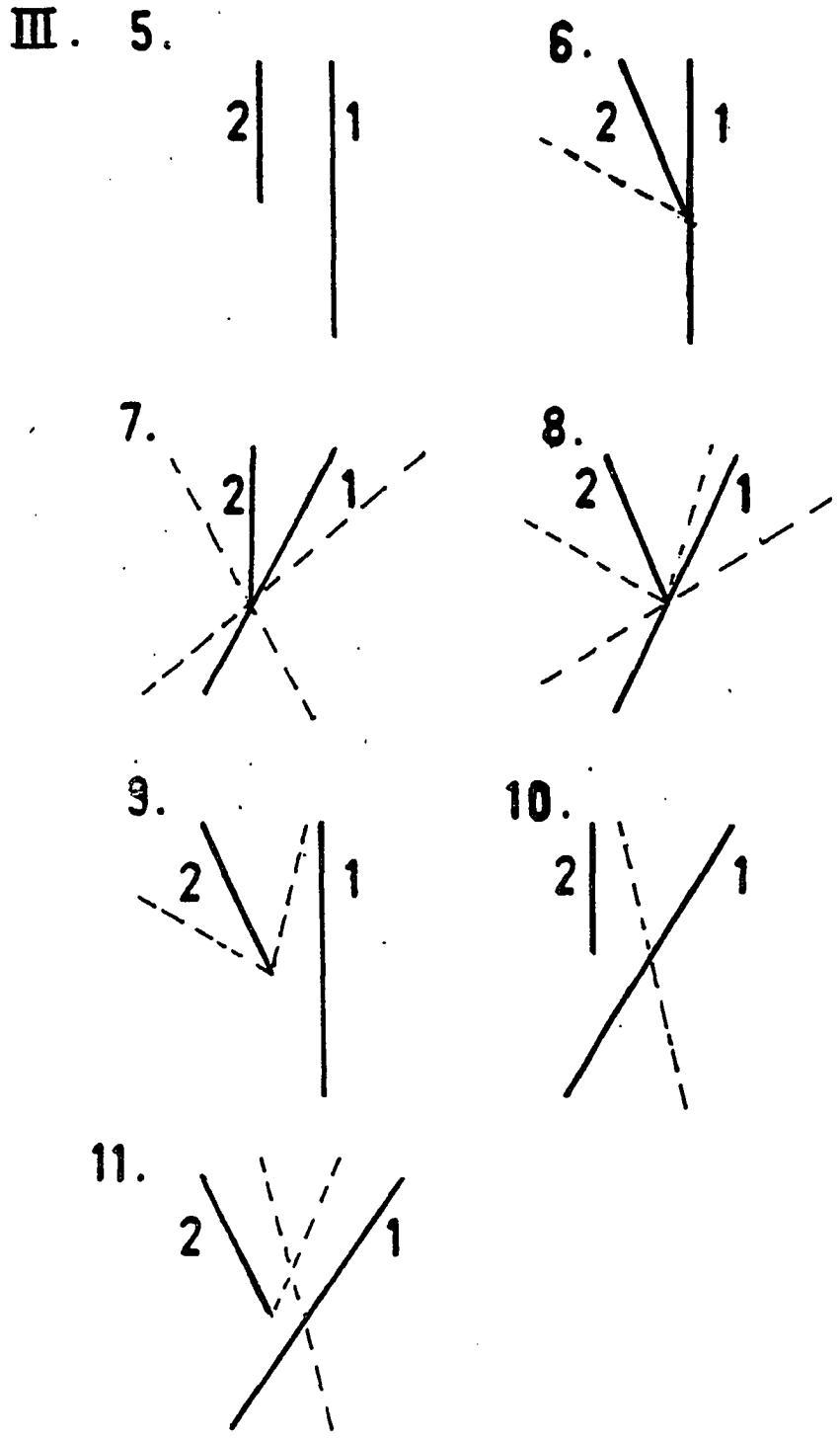


Figure 40. Hierarchical linear models

IV.

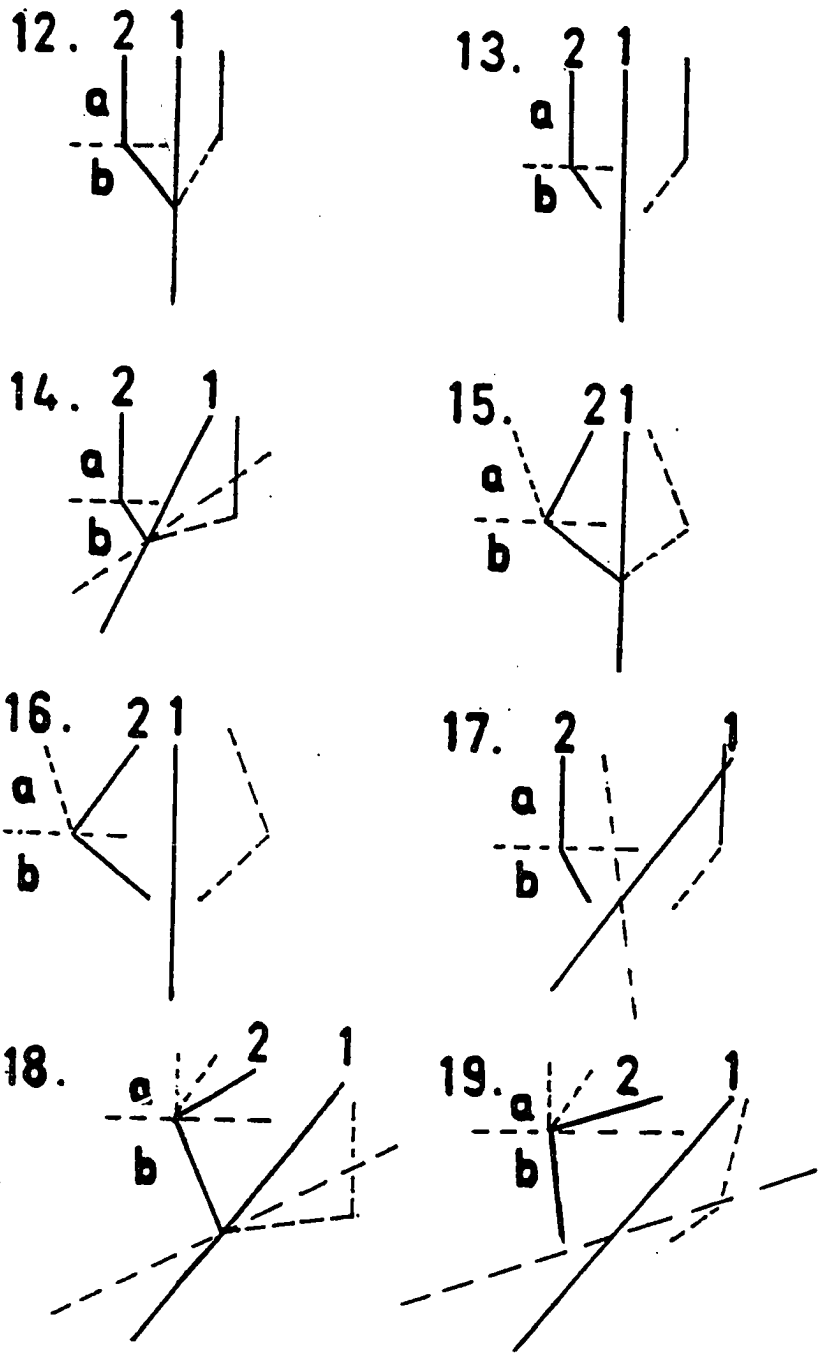


Figure 41. Hierarchical linear models

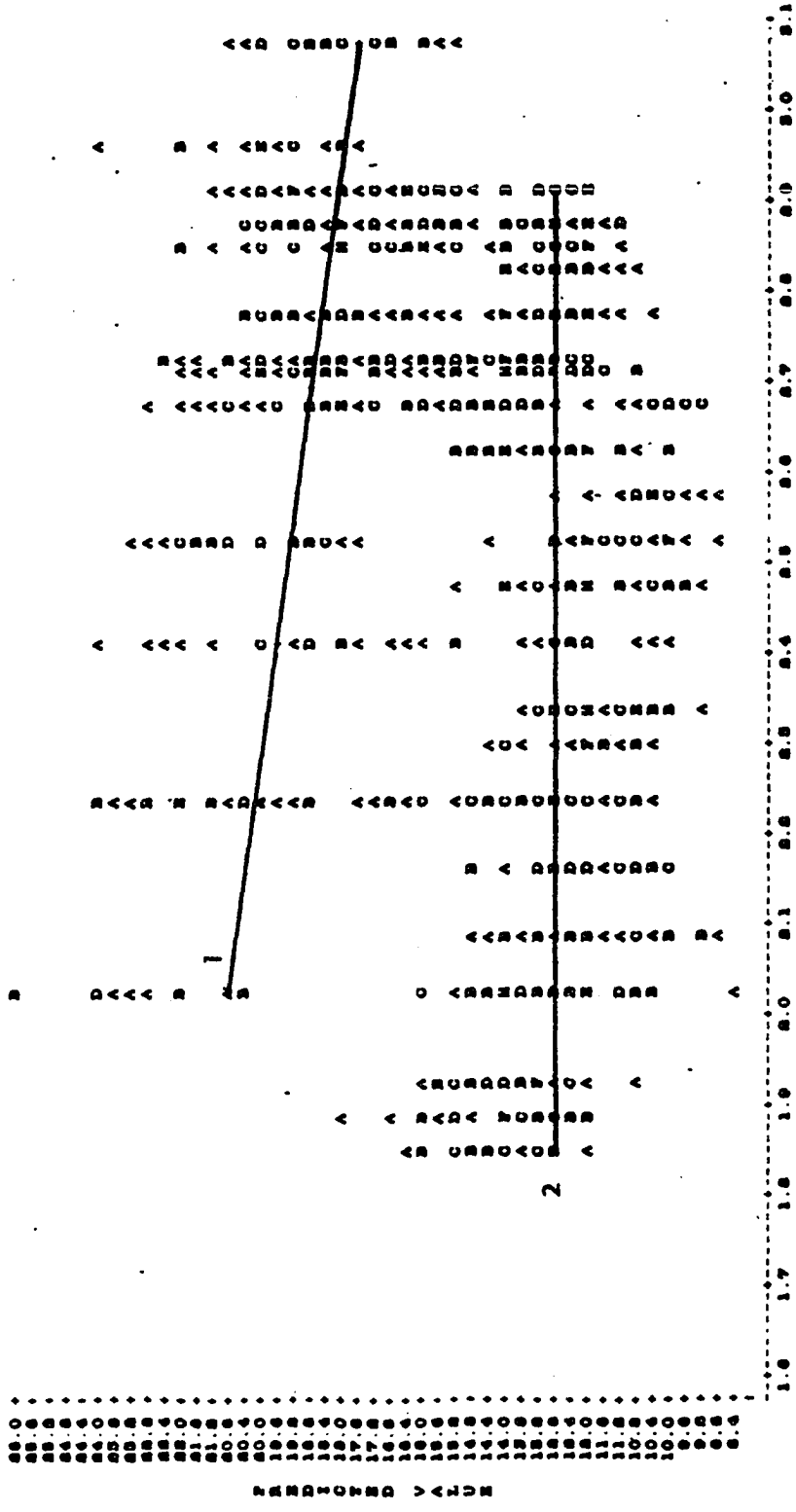


Figure 42. The solid lines indicate the best fitting linear model for the length of the apical process in the Indian Ocean sites.

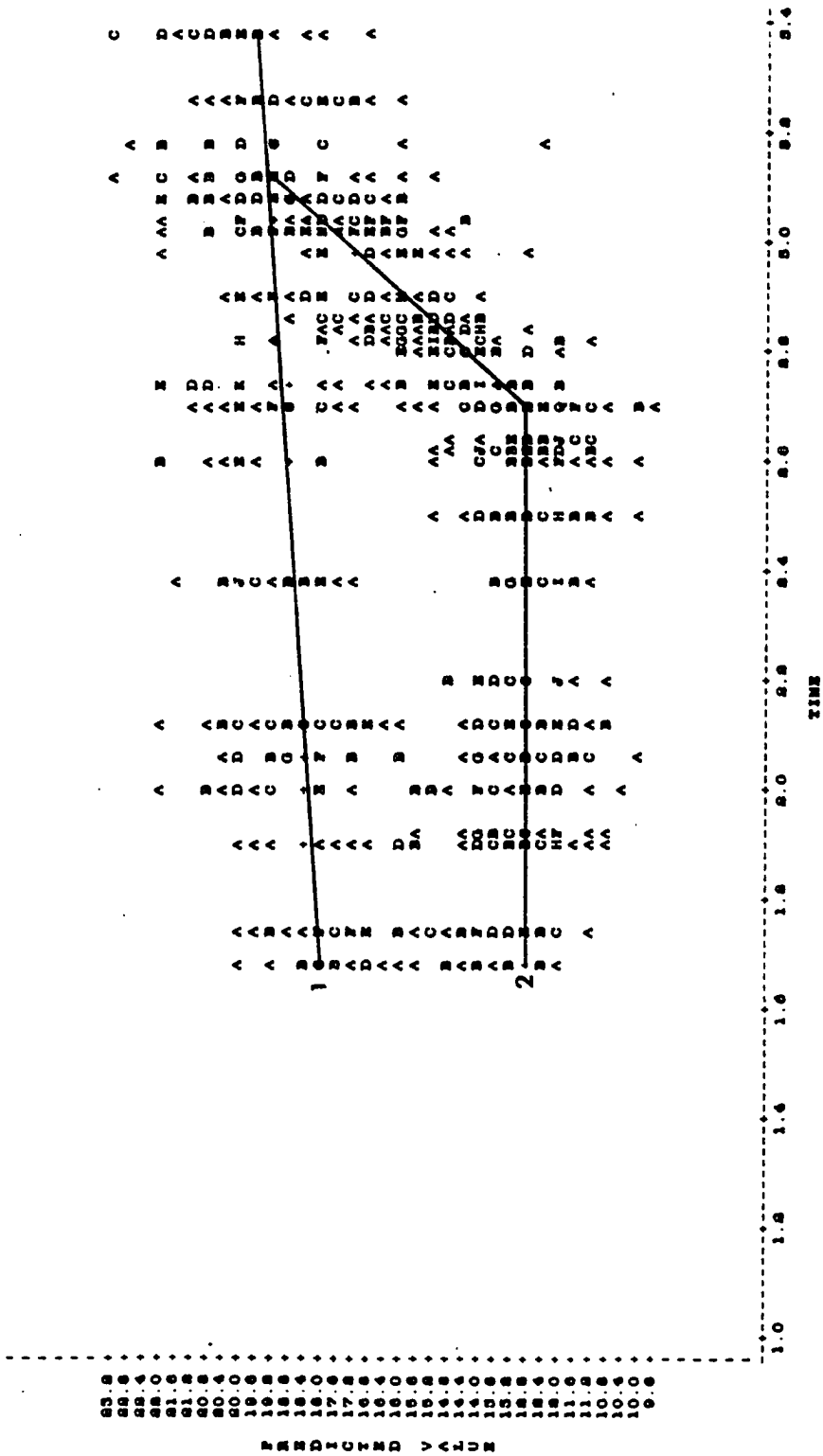


Figure 43. The solid lines indicate the best fitting linear model for the length of the apical process in site RC12-66.

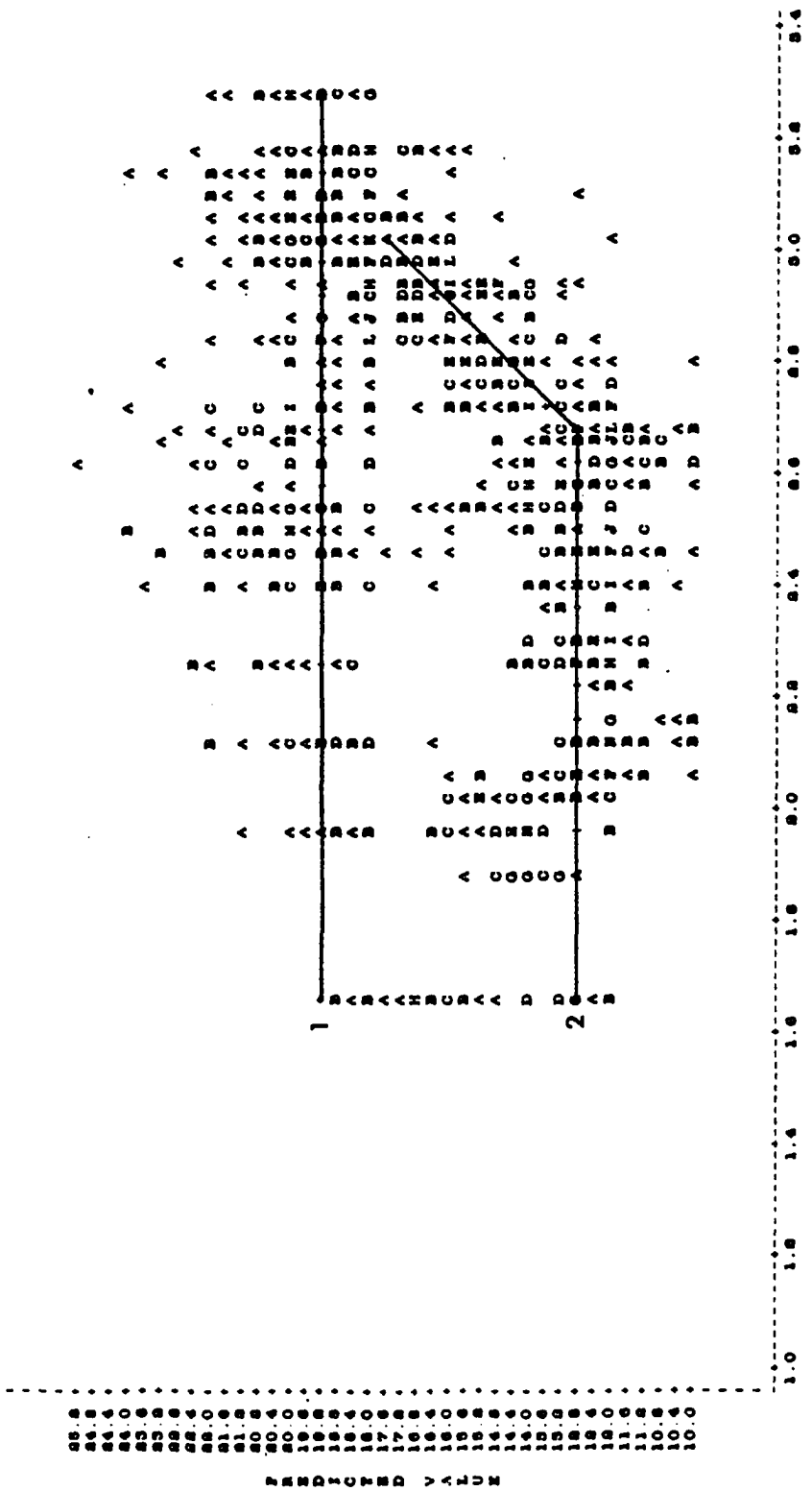


Figure 44. The solid lines indicate the best fitting linear model for the length of the apical process in DSDP site 573.

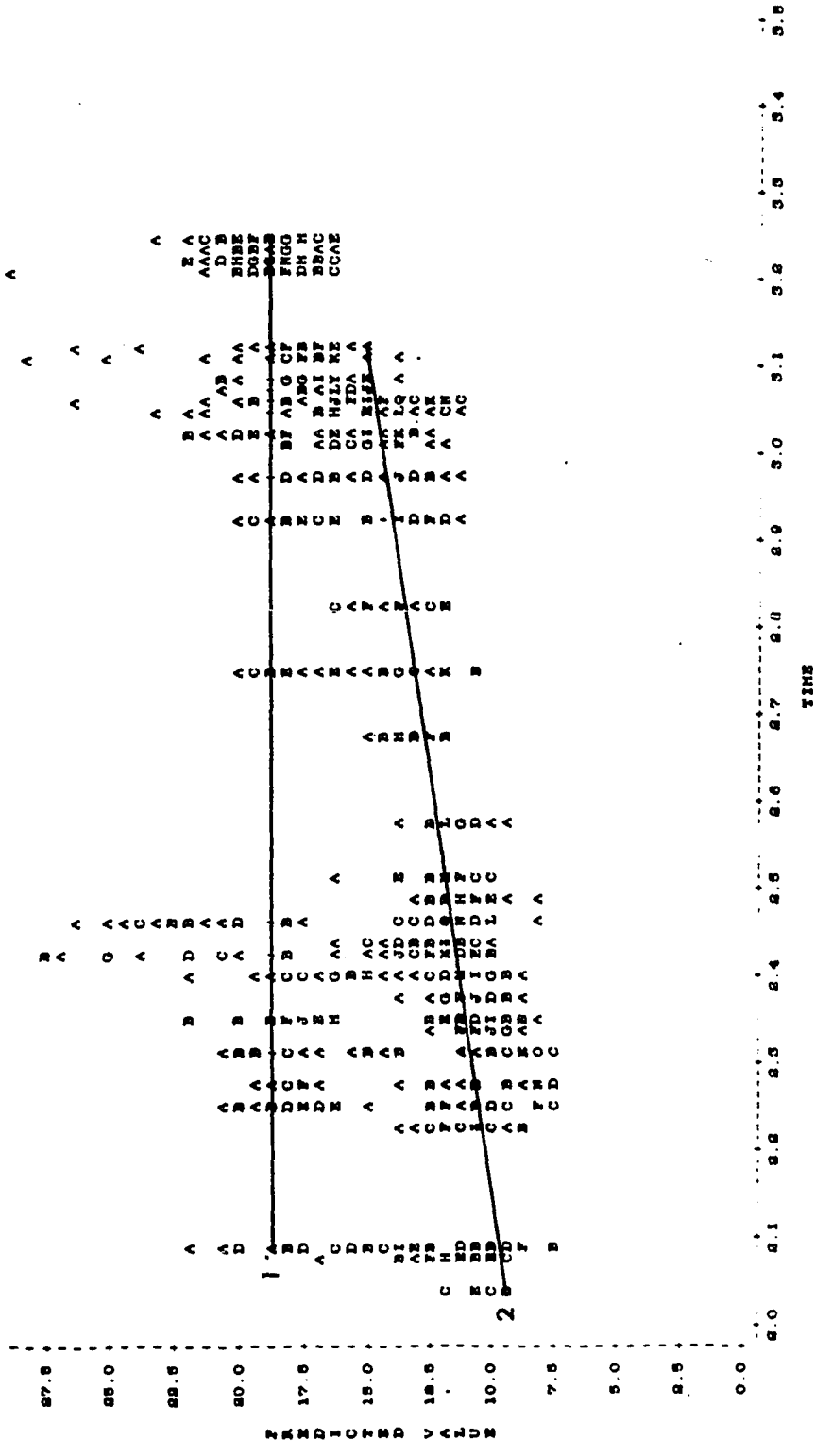


Figure 45. The solid lines indicate the best fitting linear model for the length of the apical process in DSDP site 157

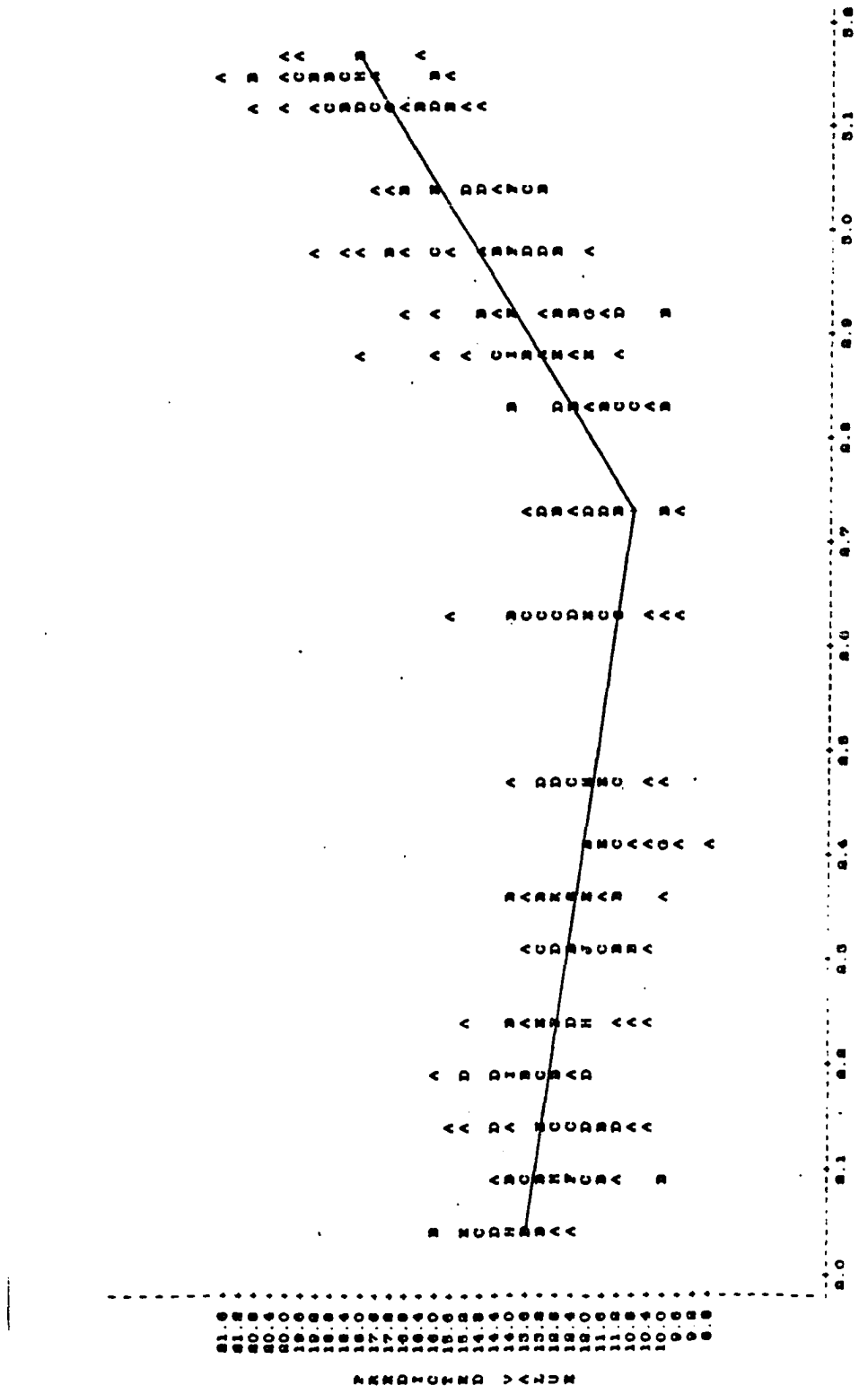


Figure 46. The solid line indicates the best fitting linear model for the length of the apical process in DSDP site 572c.

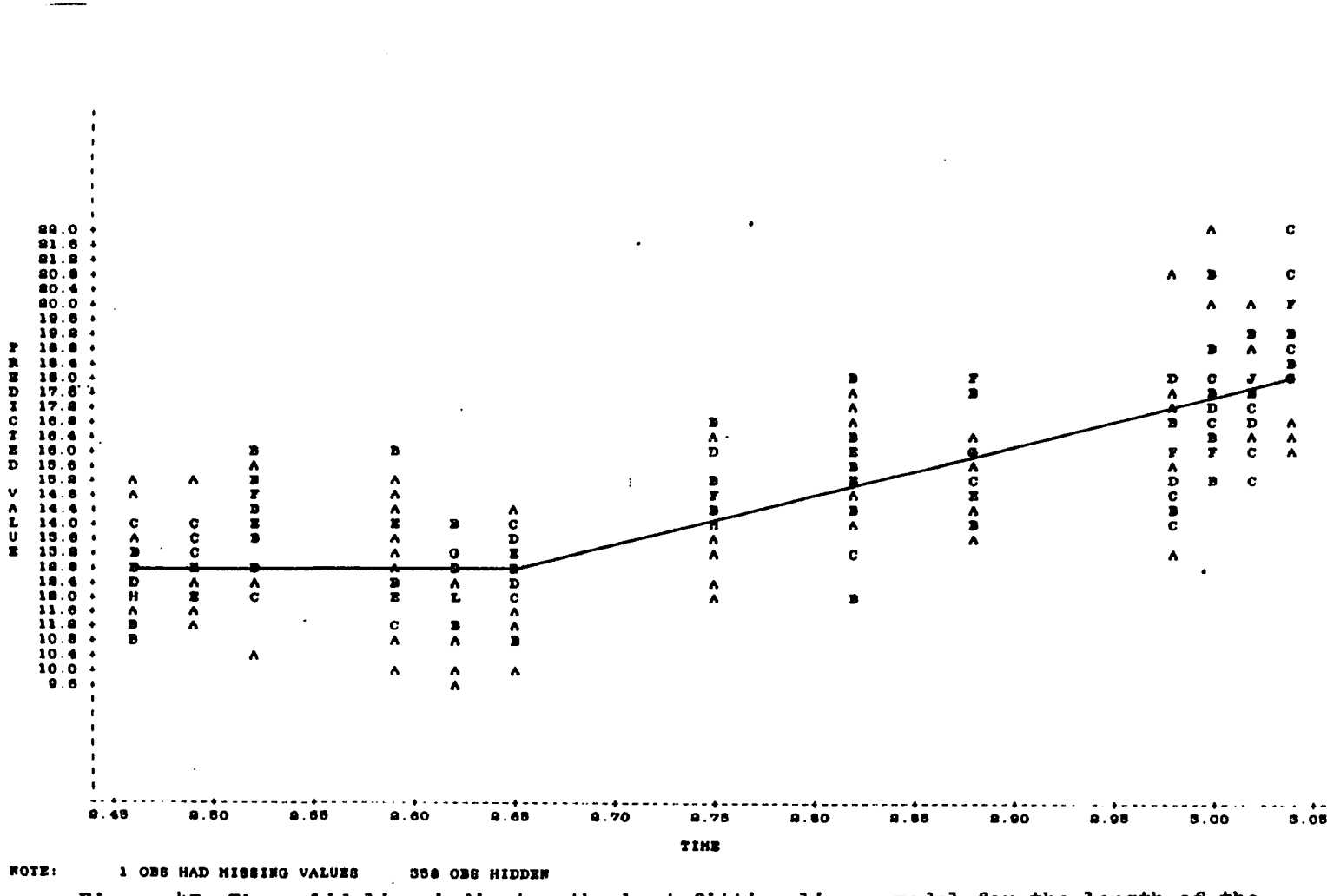


Figure 47. The solid line indicates the best fitting linear model for the length of the apical process in site V28-179.

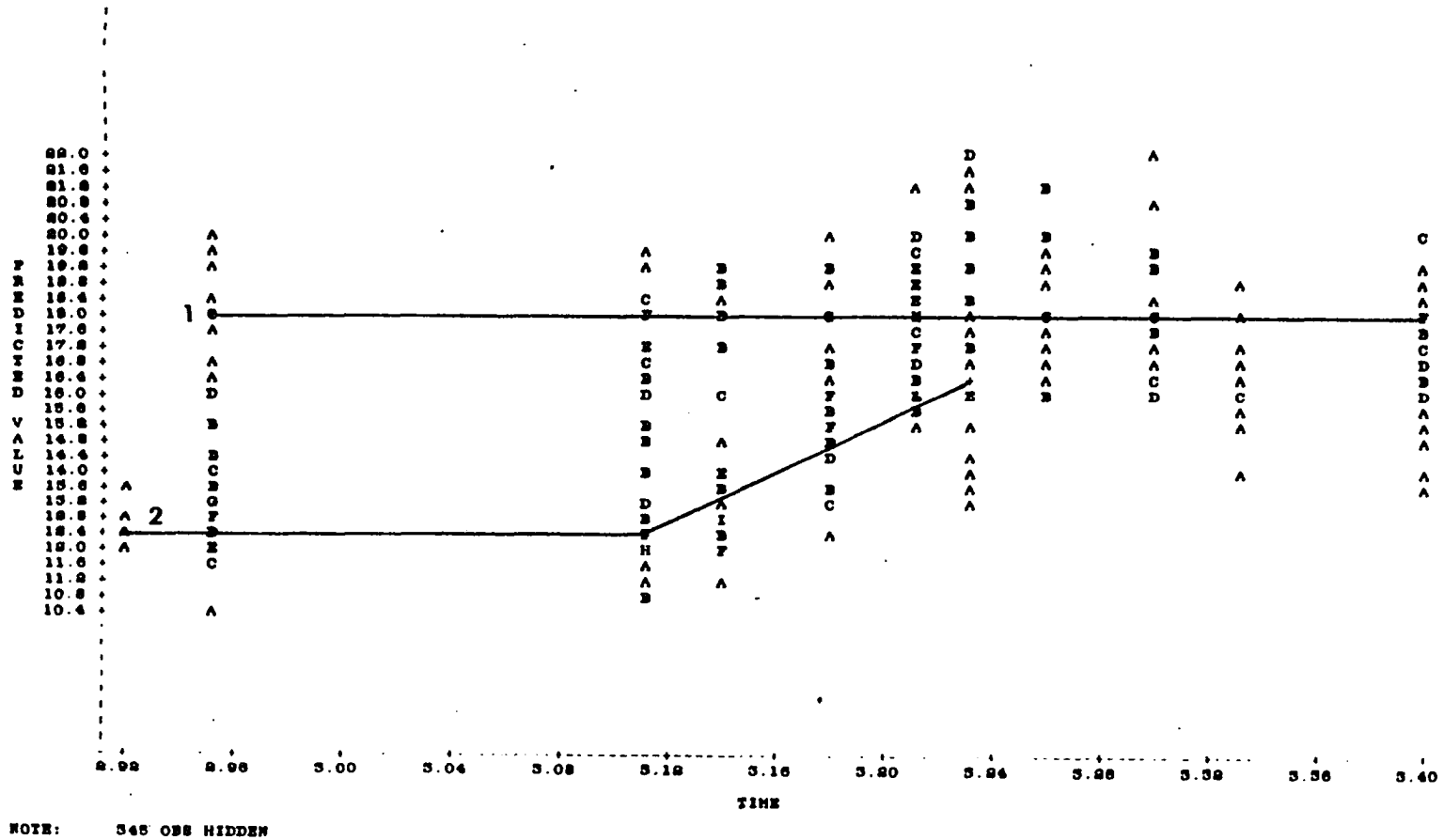


Figure 48. The solid lines indicate the best fitting linear model for the length of the apical process in DSDP site 504.

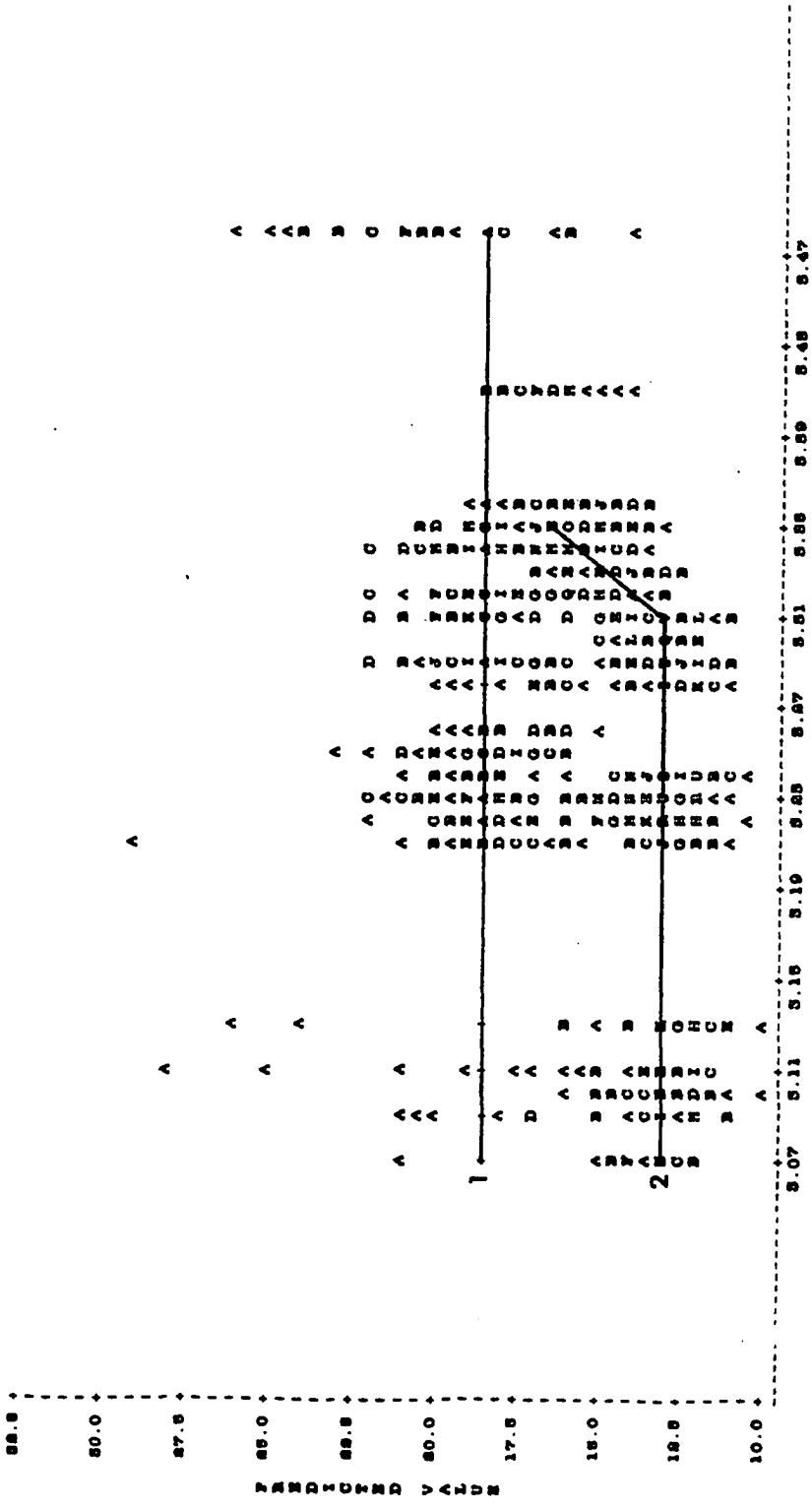


Figure 49. The solid lines indicate the best fitting linear model for the length of the apical process in DSDP site 157.

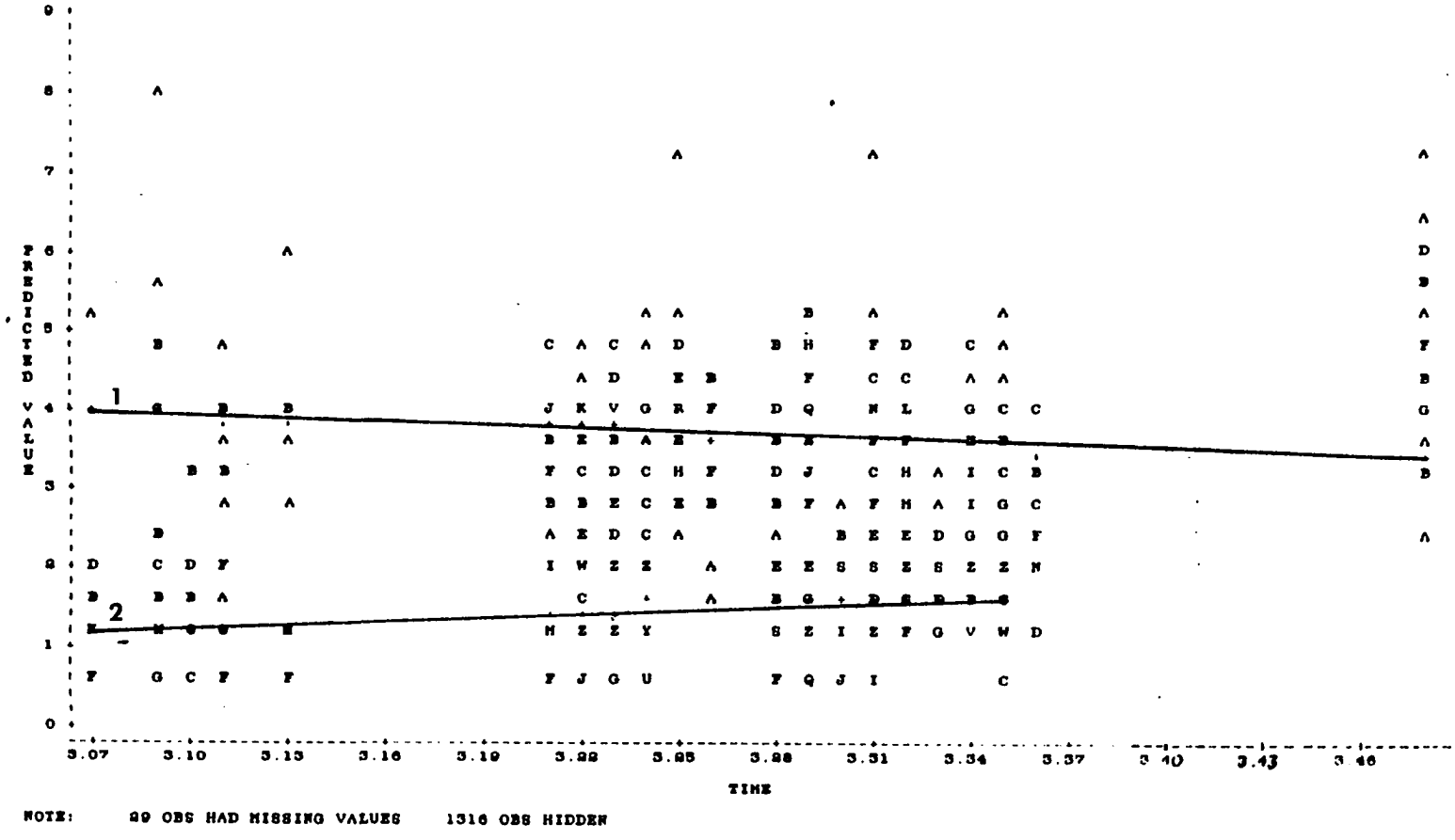


Figure 50. The solid lines indicate the best fitting model for the height of the hyaline area in DSDP site 157.

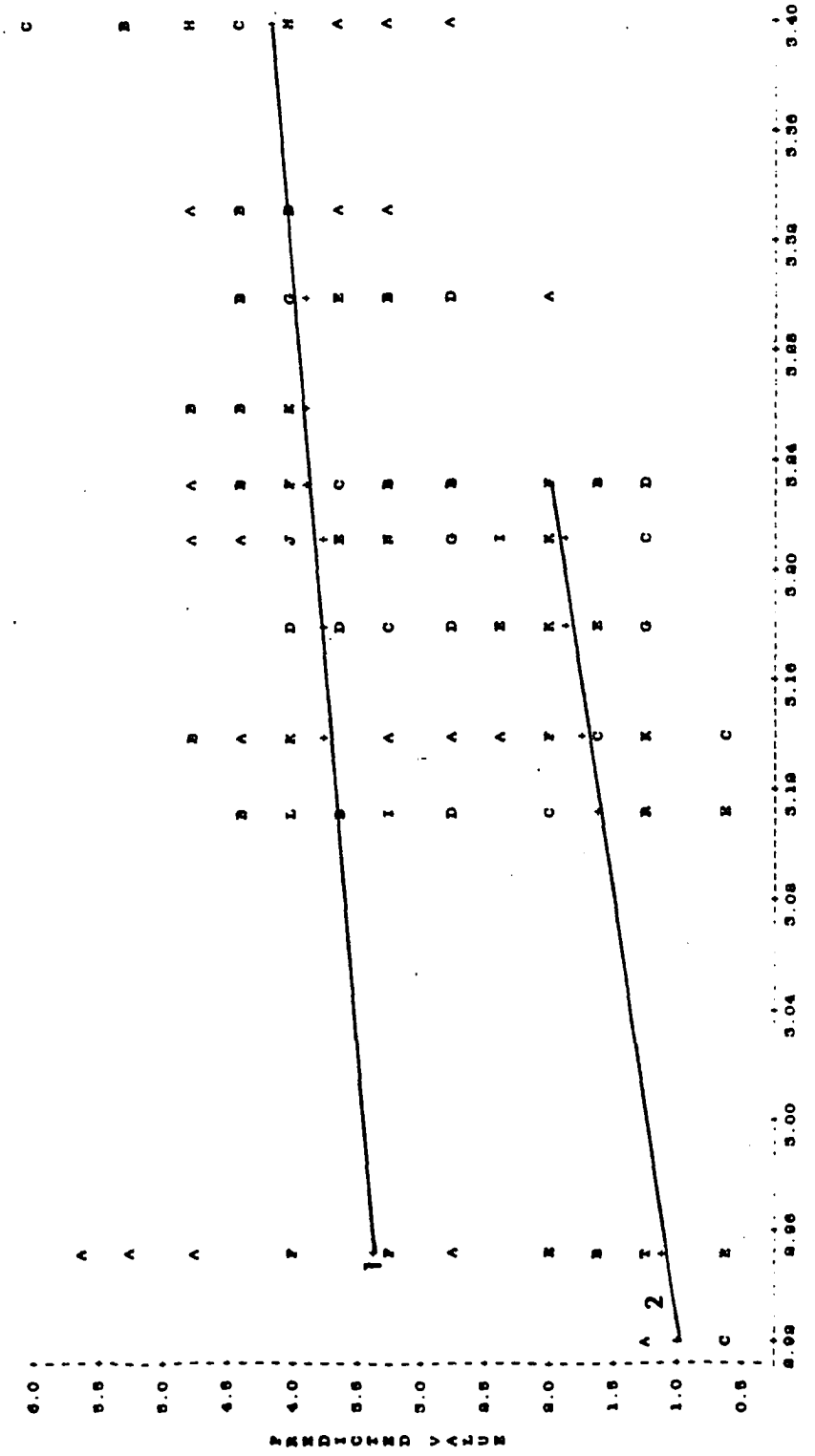


Figure 51. The solid lines indicate the best fitting model for the height of the hyaline area in DSDP site 504.

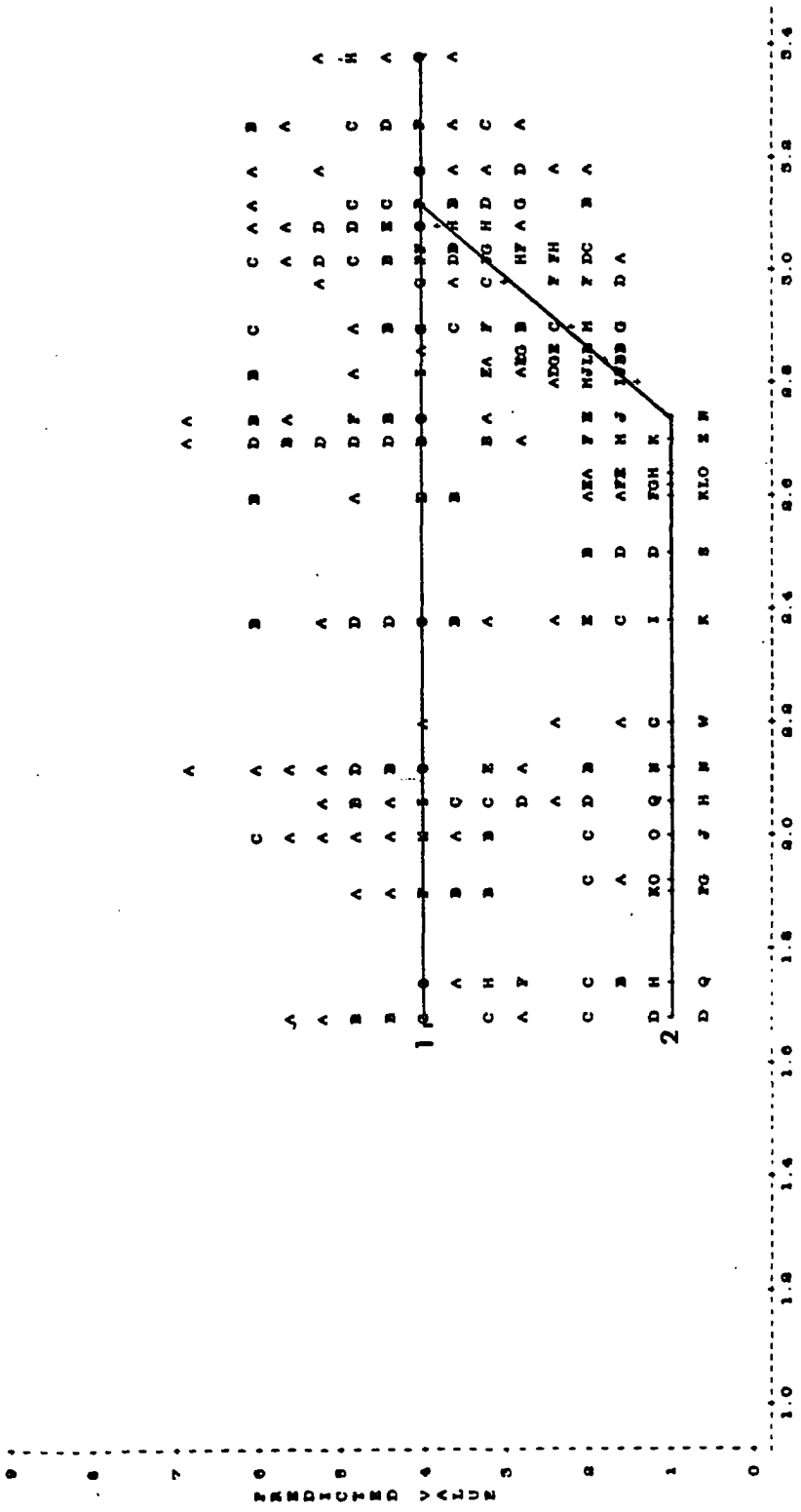


Figure 52. The solid lines indicate the best fitting model for the height of the hyaline area in site RC12-66.

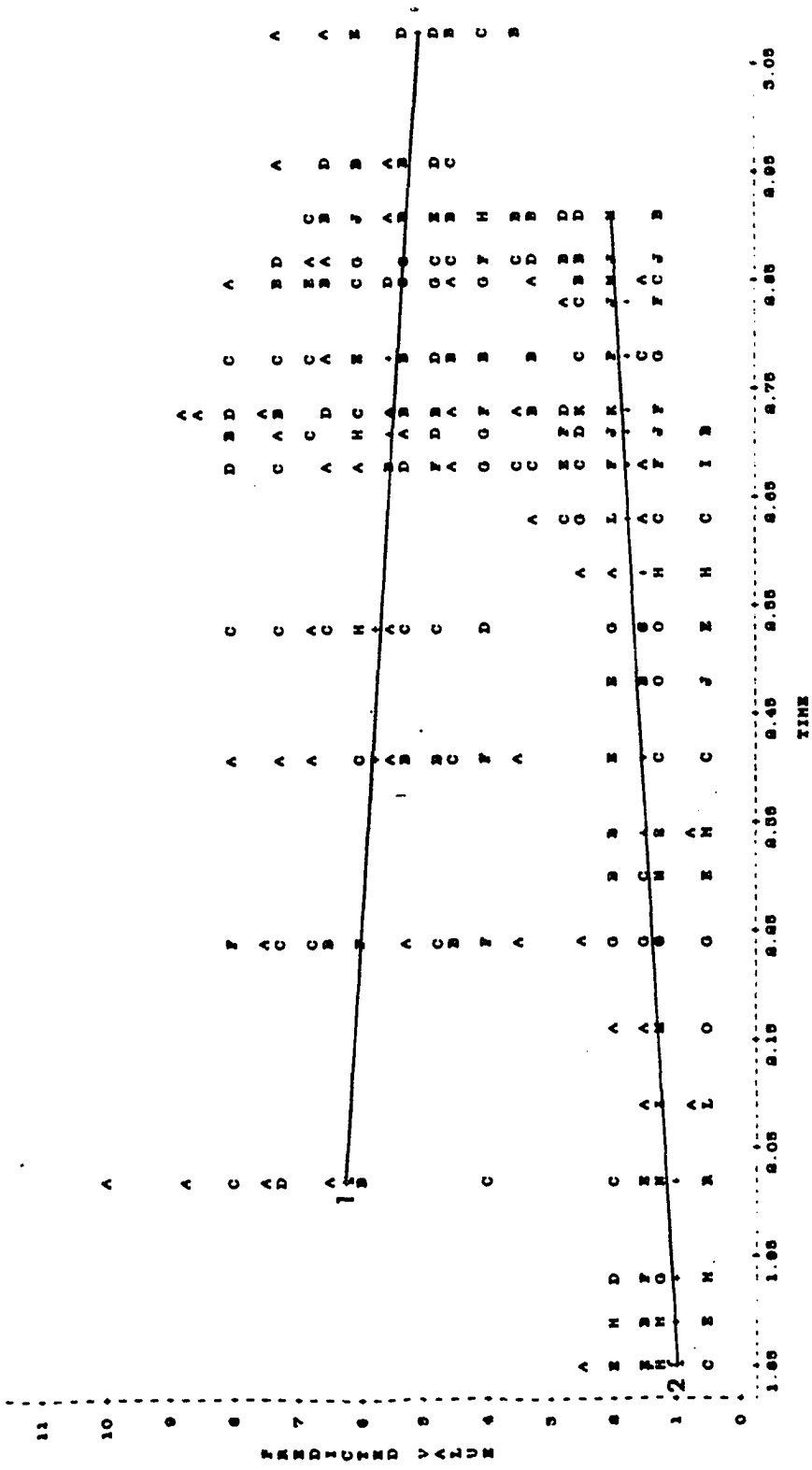


Figure 53. The solid lines indicate the best fitting model for the height of the hyaline area in the Indian Ocean sites.

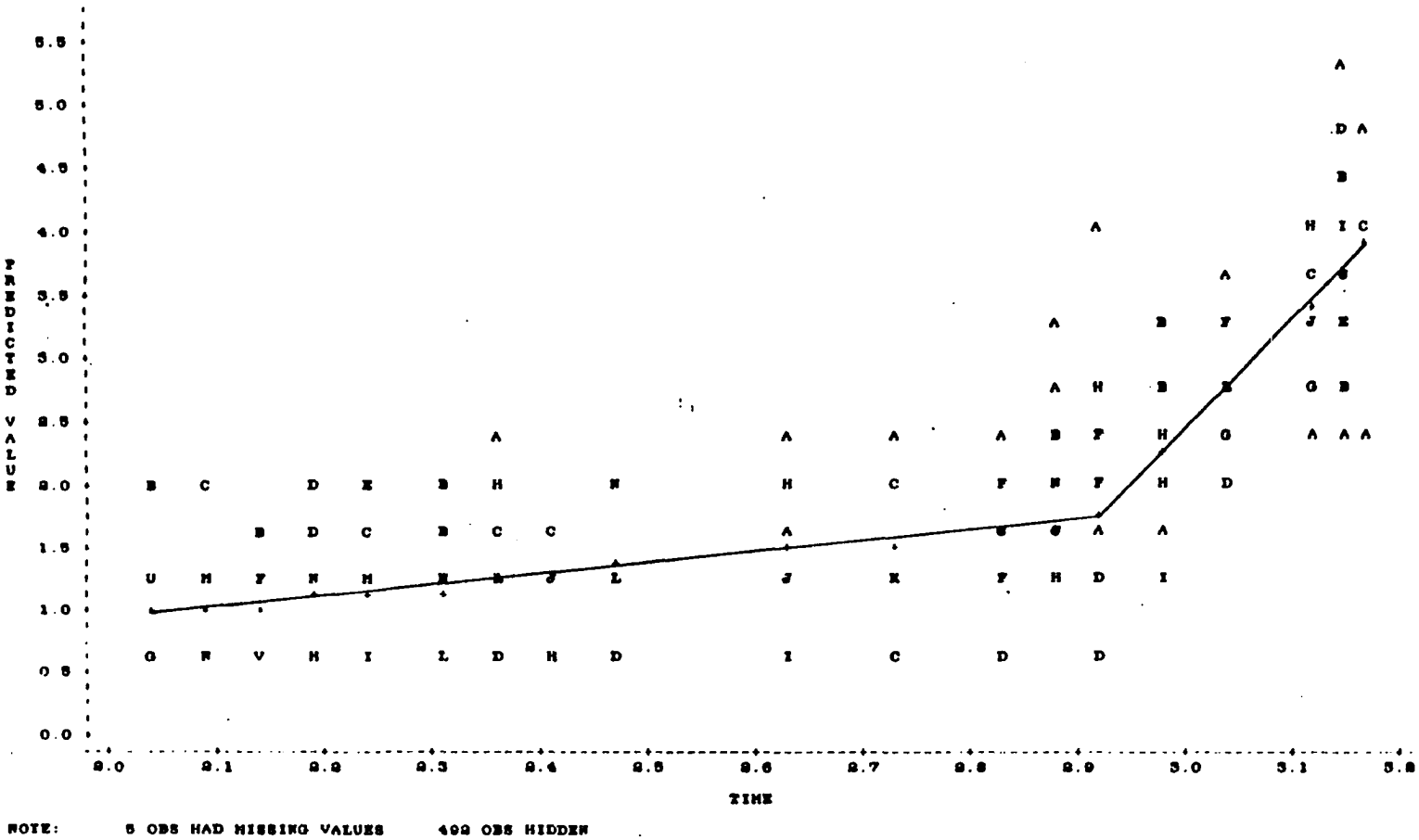


Figure 54. The solid line indicates the best fitting model for the height of the hyaline area in DSDP site 572c.

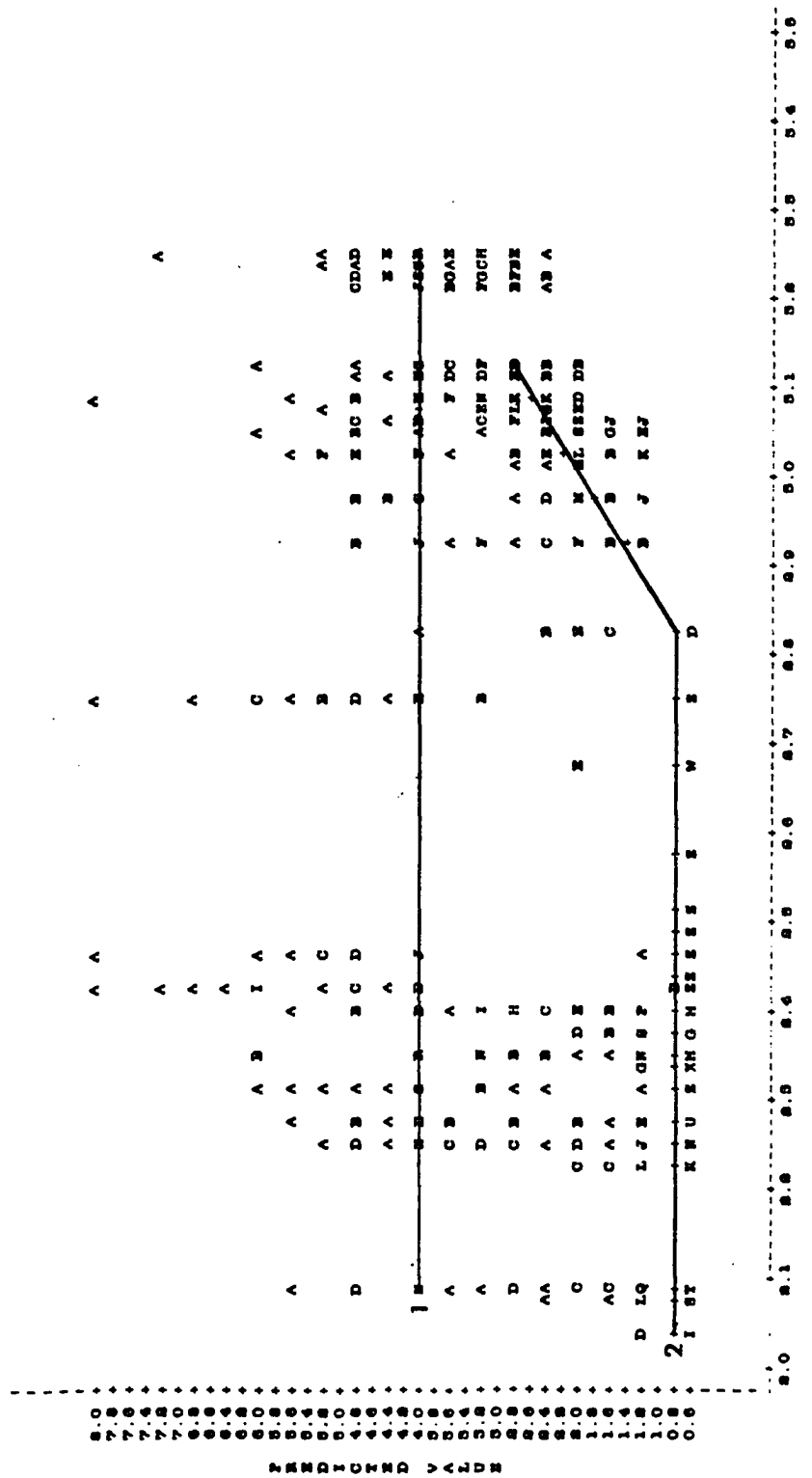


Figure 55. The solid lines indicate the best fitting linear model for the height of the hyaline area in DSDP site 157.

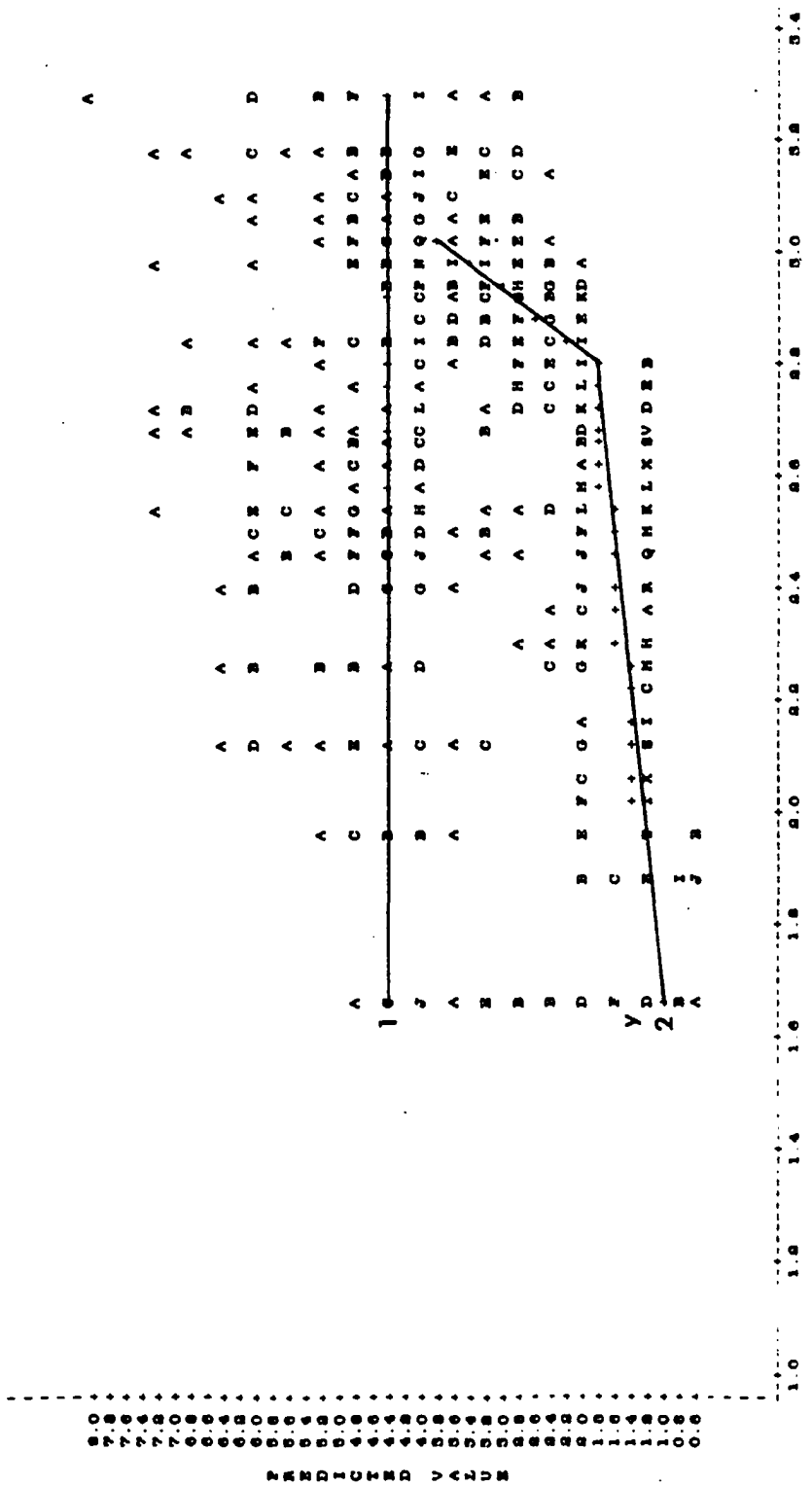
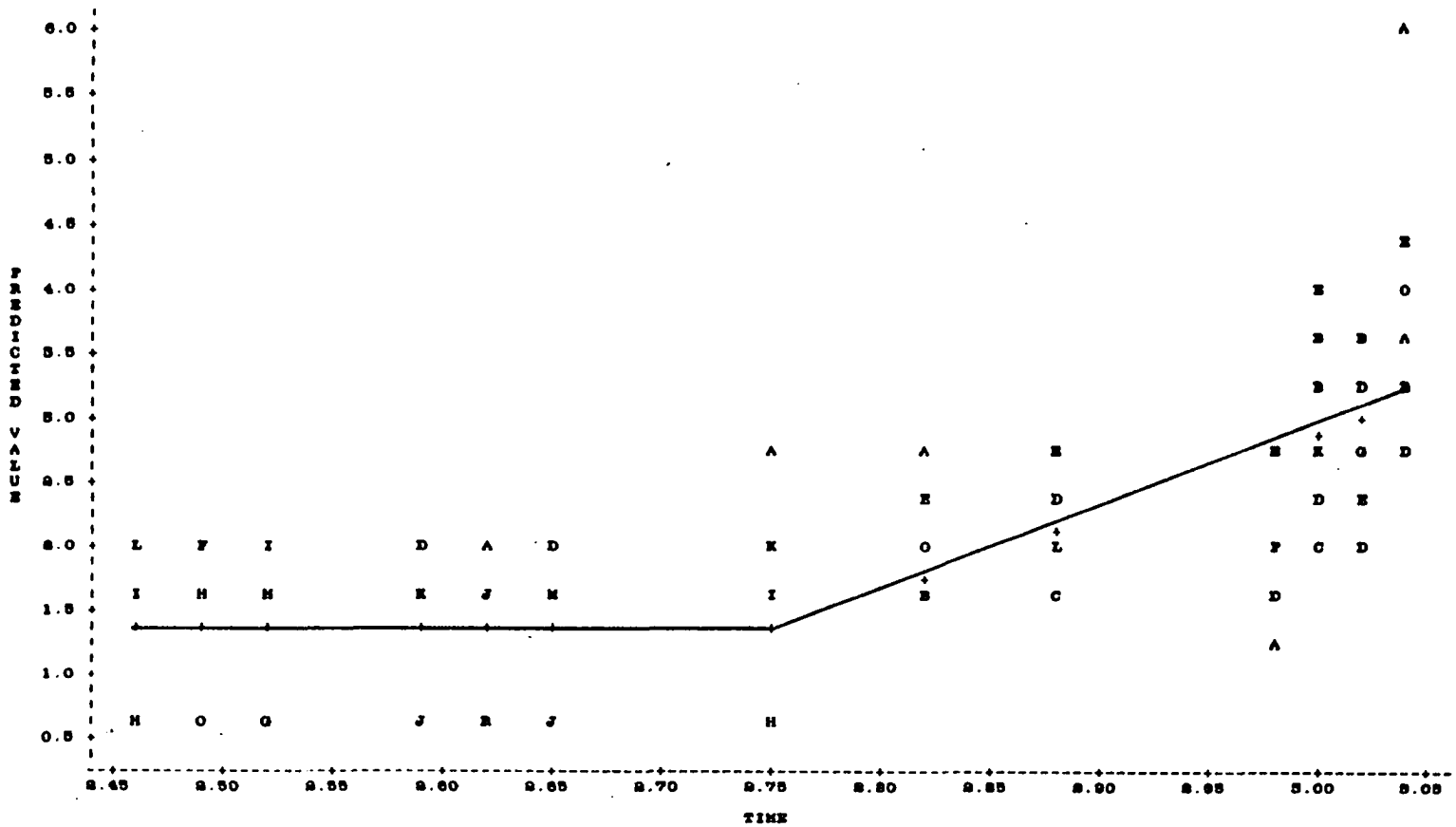


Figure 56. The solid lines indicate the best fitting linear model for the height of the hyaline area in DSDP site 573.



NOTE: 24 OBS HAD MISSING VALUES 358 OBS HIDDEN

Figure 57. The solid line indicates the best fitting linear model for the height of the hyaline area in site V28-179

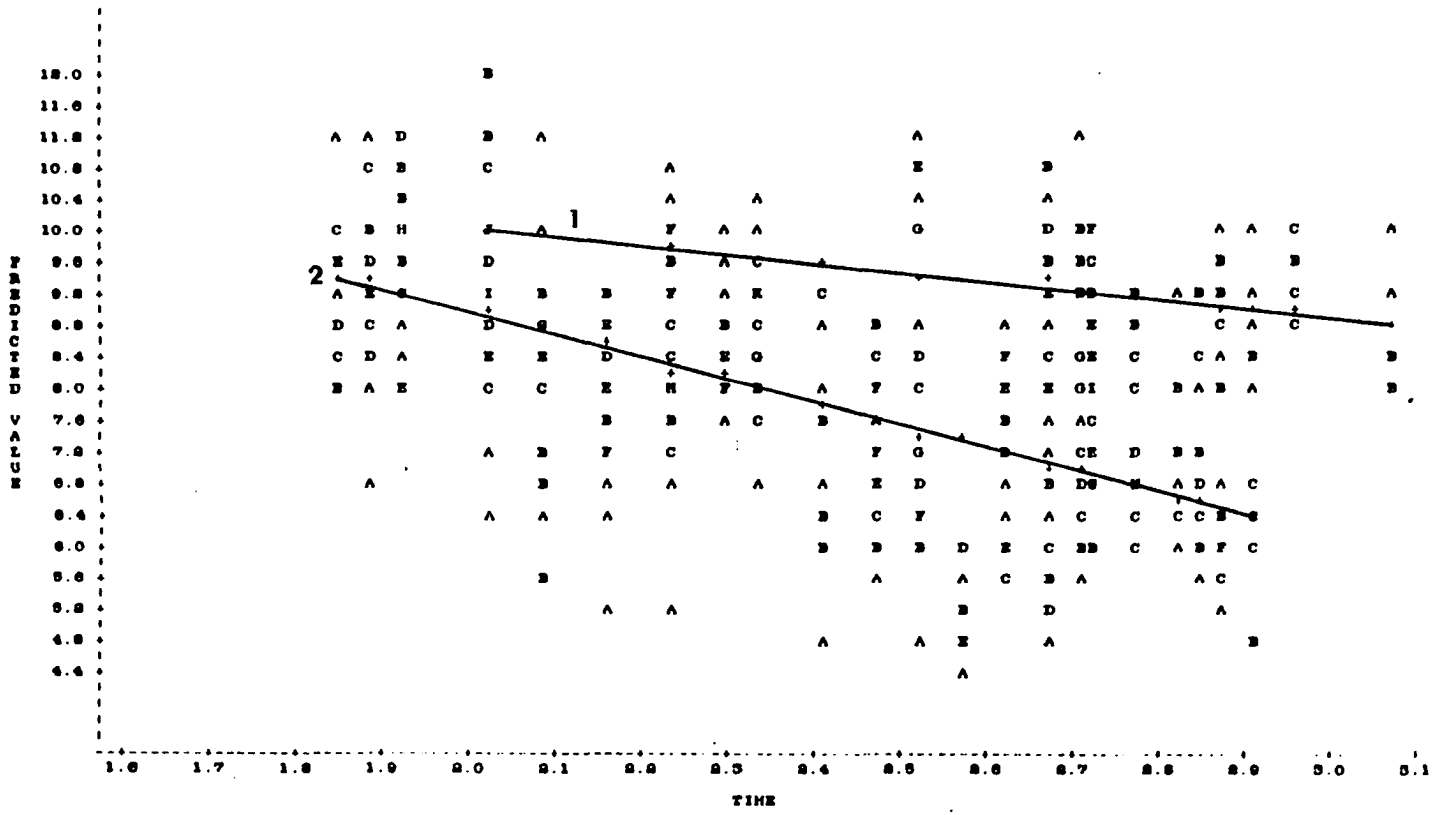


Figure 58. The solid lines indicate the best fitting model for the width of the valve in the Indian Ocean sites.

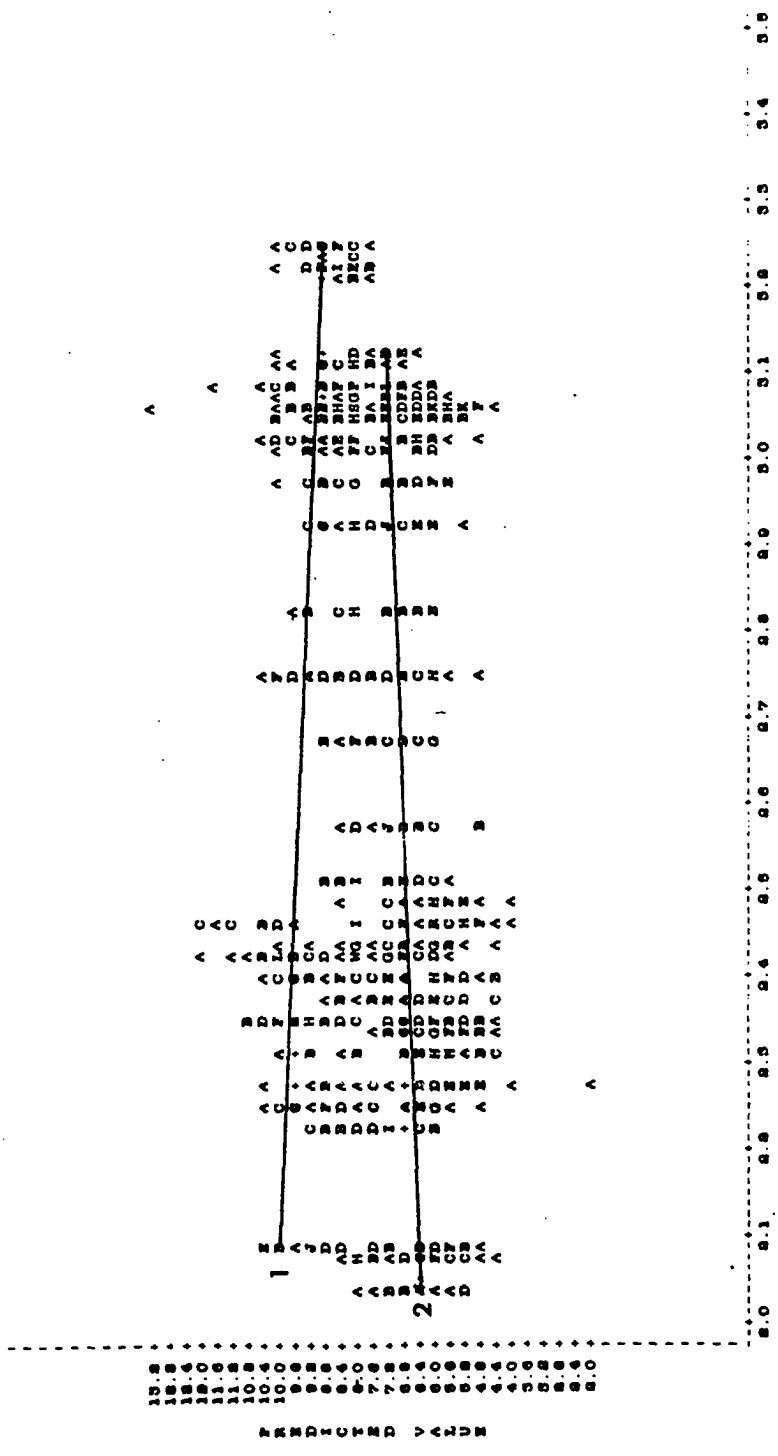


Figure 59. The solid lines indicate the the best fitting linear model for the width of the valve in DSDP site 157.

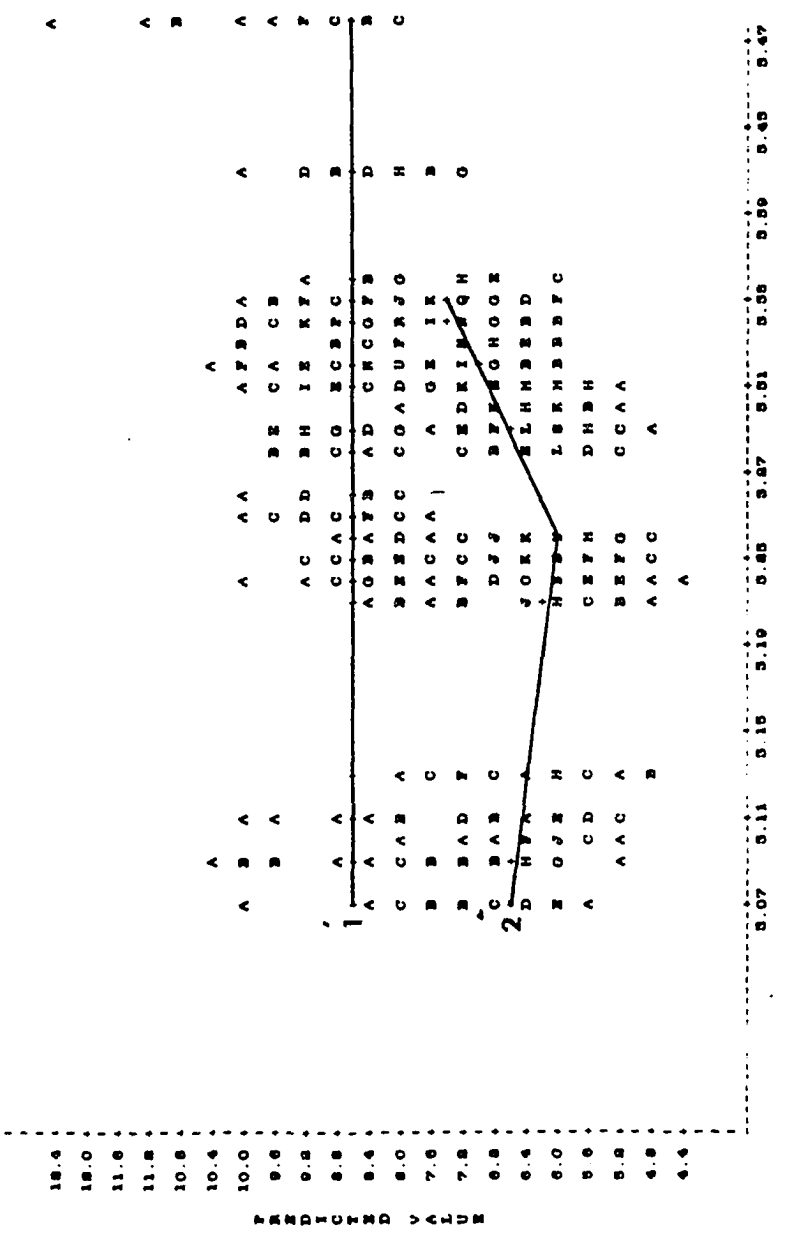


Figure 60. The solid lines indicate the best fitting linear model for the width of the valve in DSDP site 157.

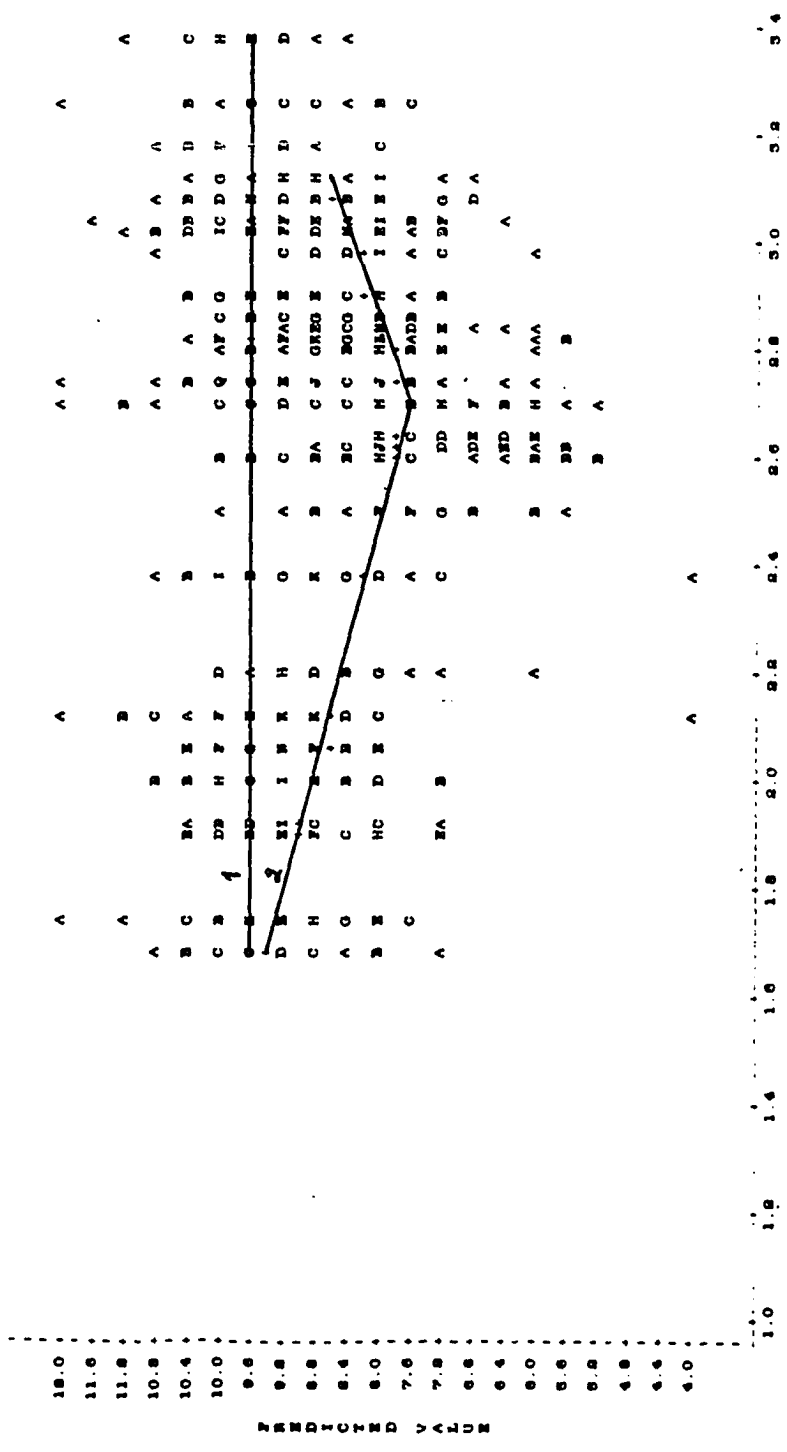


Figure 61. The solid lines indicate the best fitting linear model for the width of the valve in site RC12-66.

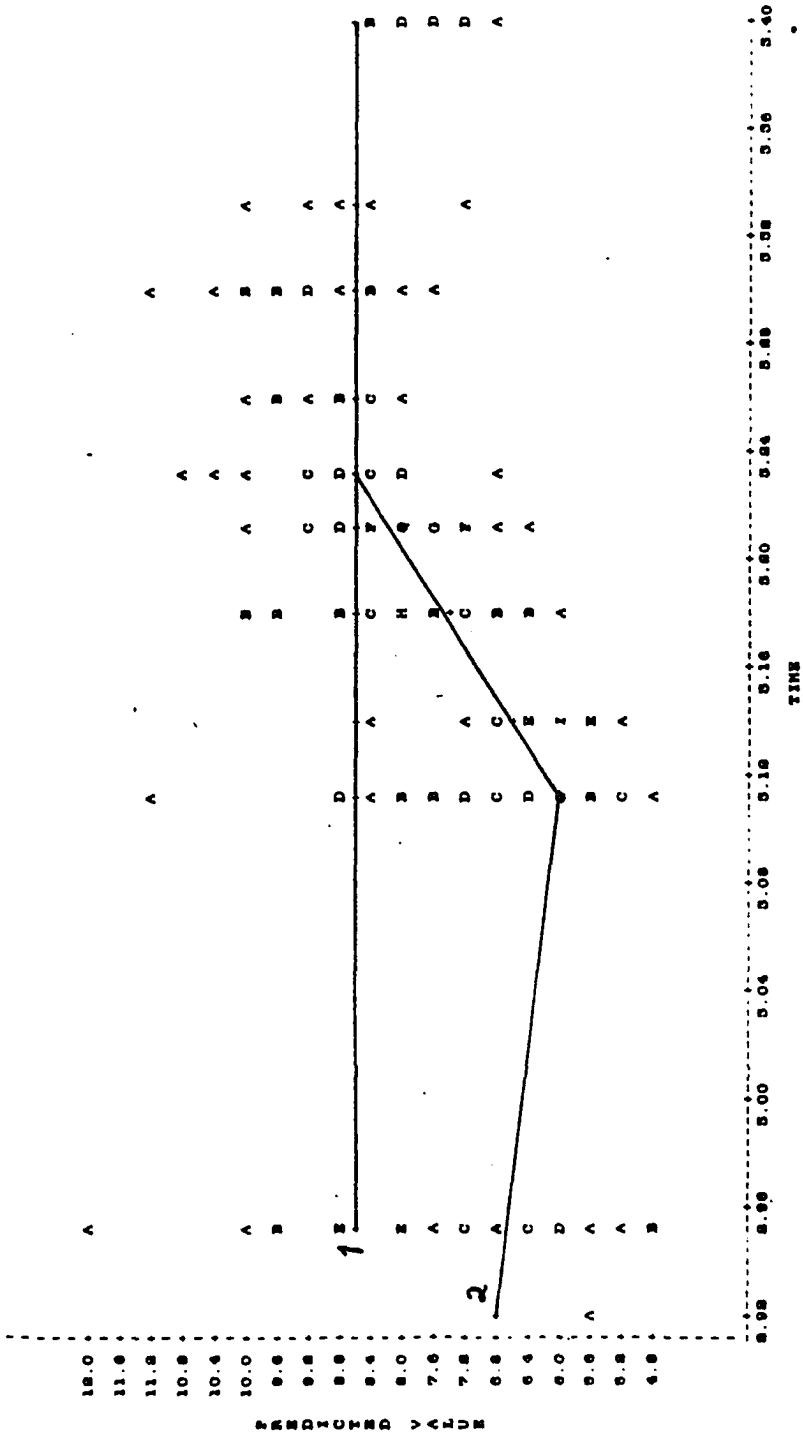


Figure 62. The solid lines indicate the best fitting model for the width of the valve in DSDP site 504.

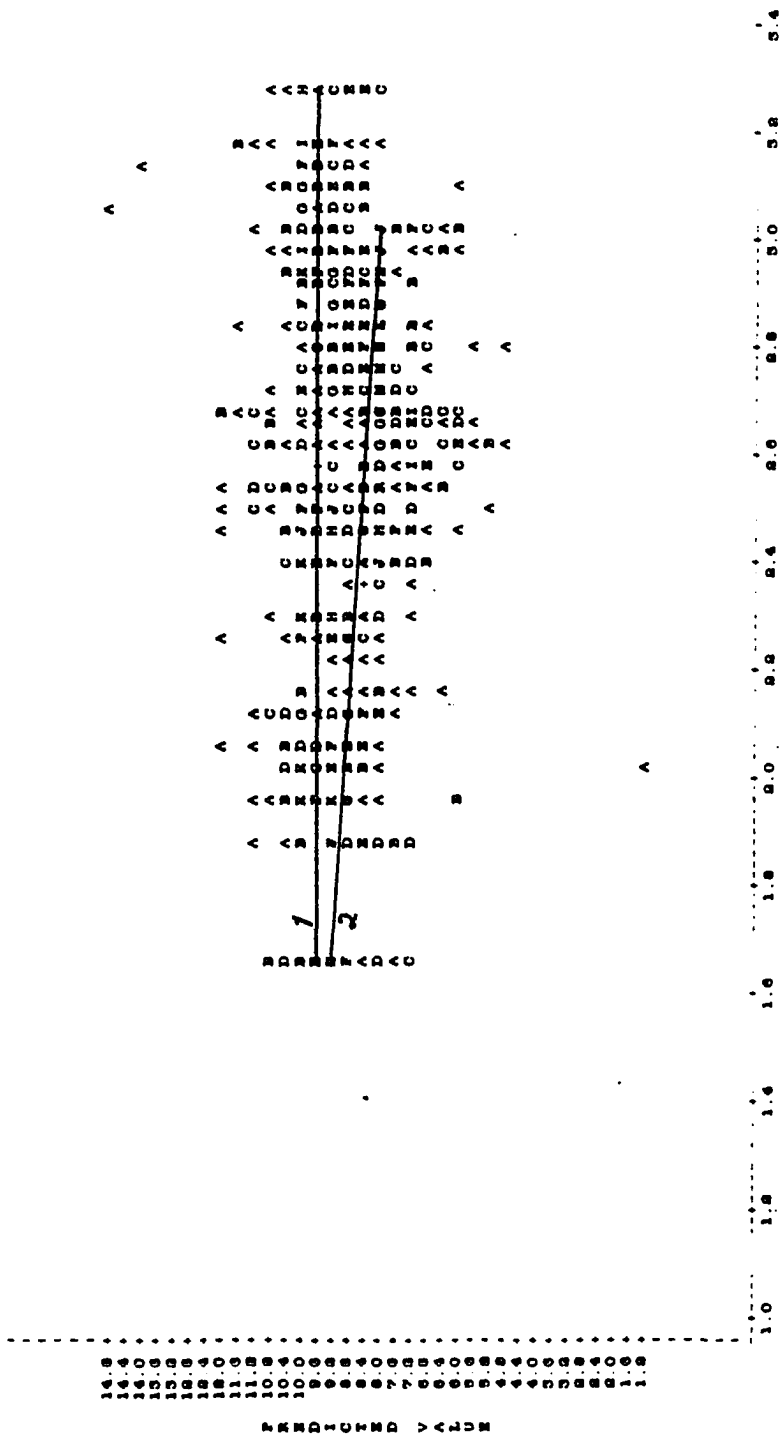


Figure 63. The solid lines indicate the best fitting model for the width of the valve in DSDP site 573.

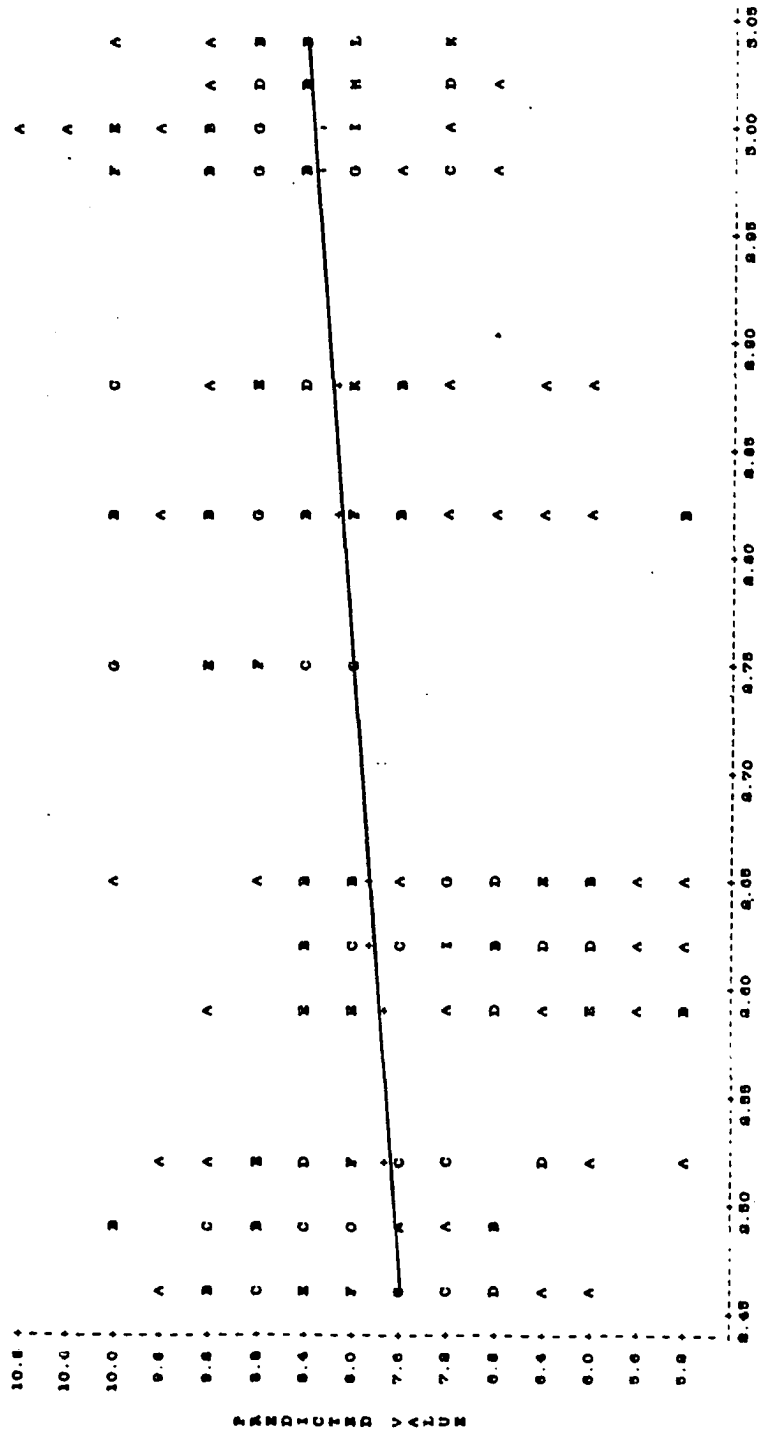


Figure 64. The solid lines indicate the best fitting model for the width of the valve in site V28-179.

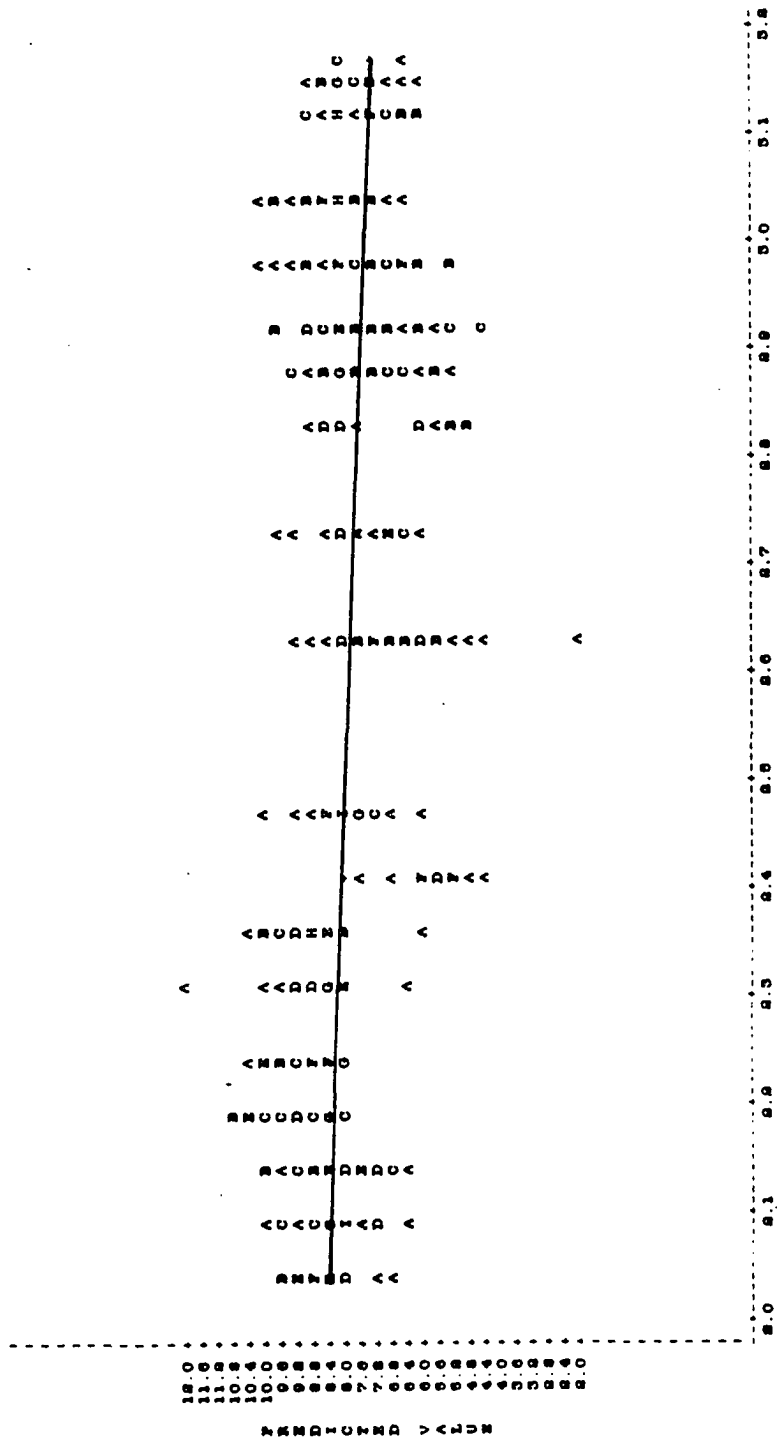


Figure 65. The solid line indicates the best fitting model for the width of the valve in DSDP site 572c.

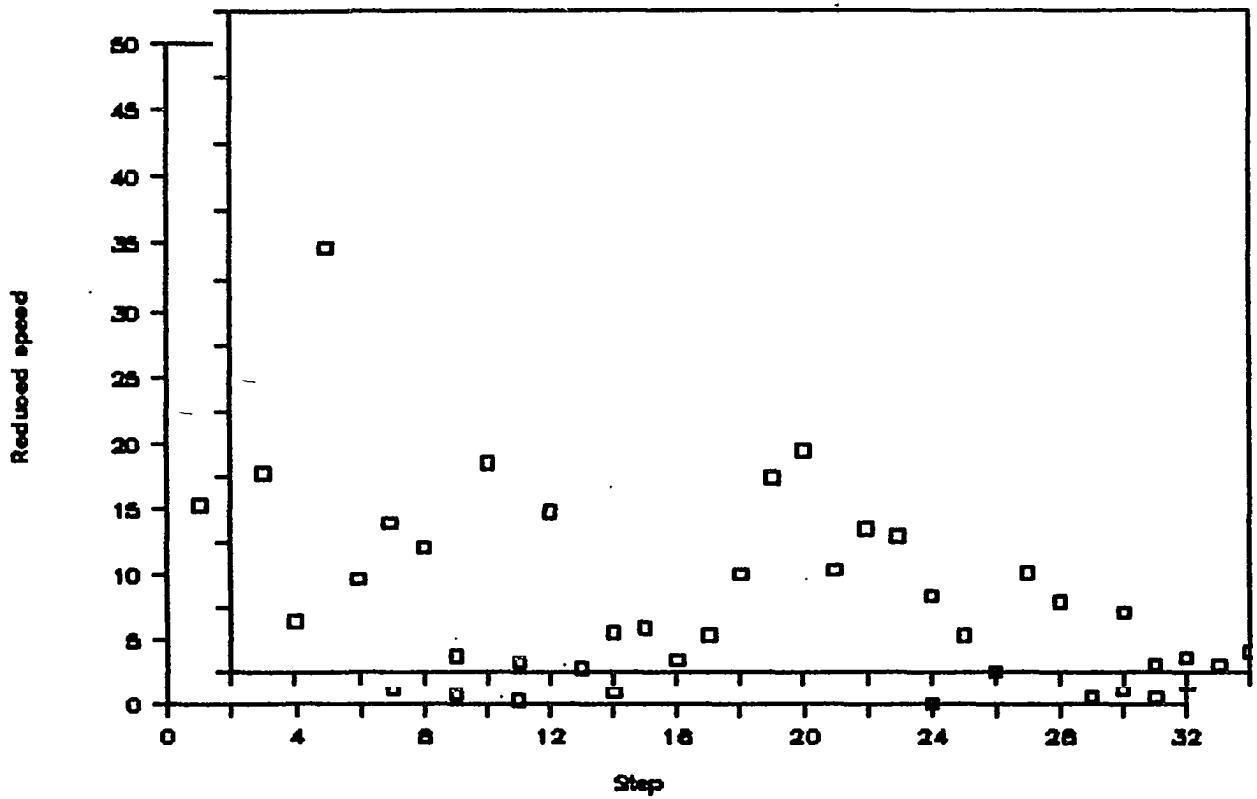


Figure 66. Reduced speeds for the length of the apical process in R.bergonii in DSDP site 157.

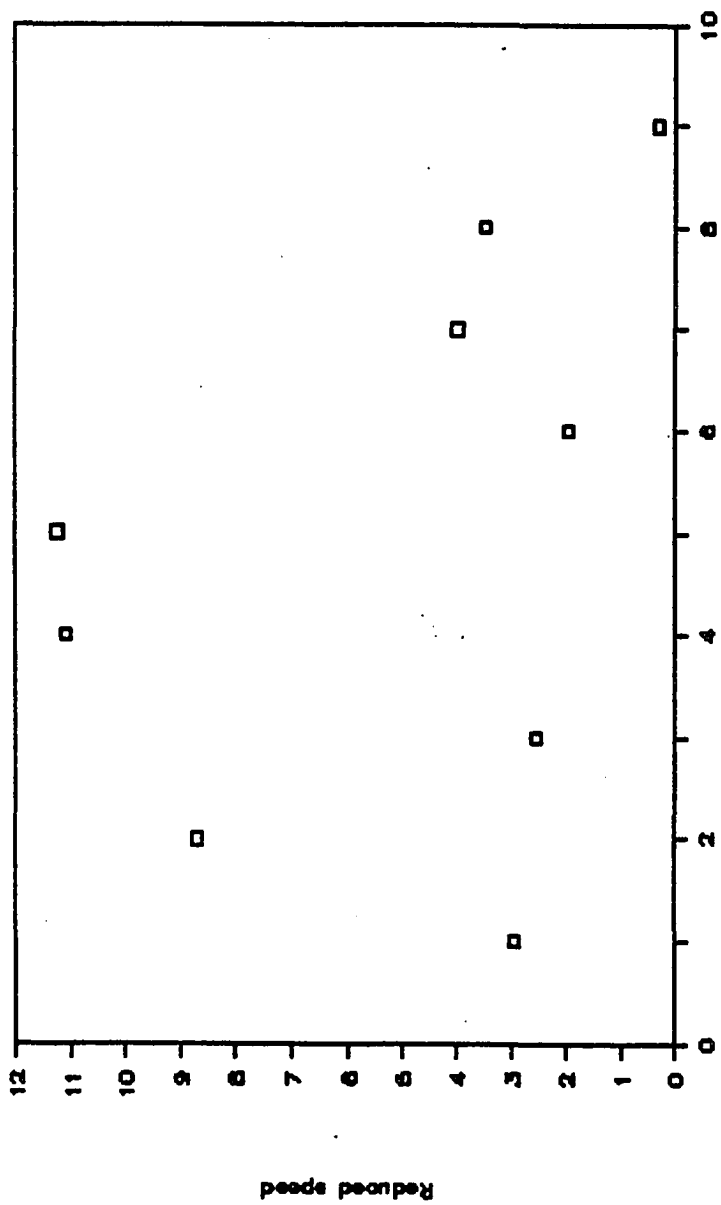


Figure 67. Reduced speeds for the length of the apical process in R.bergonii in DSDP site 504.

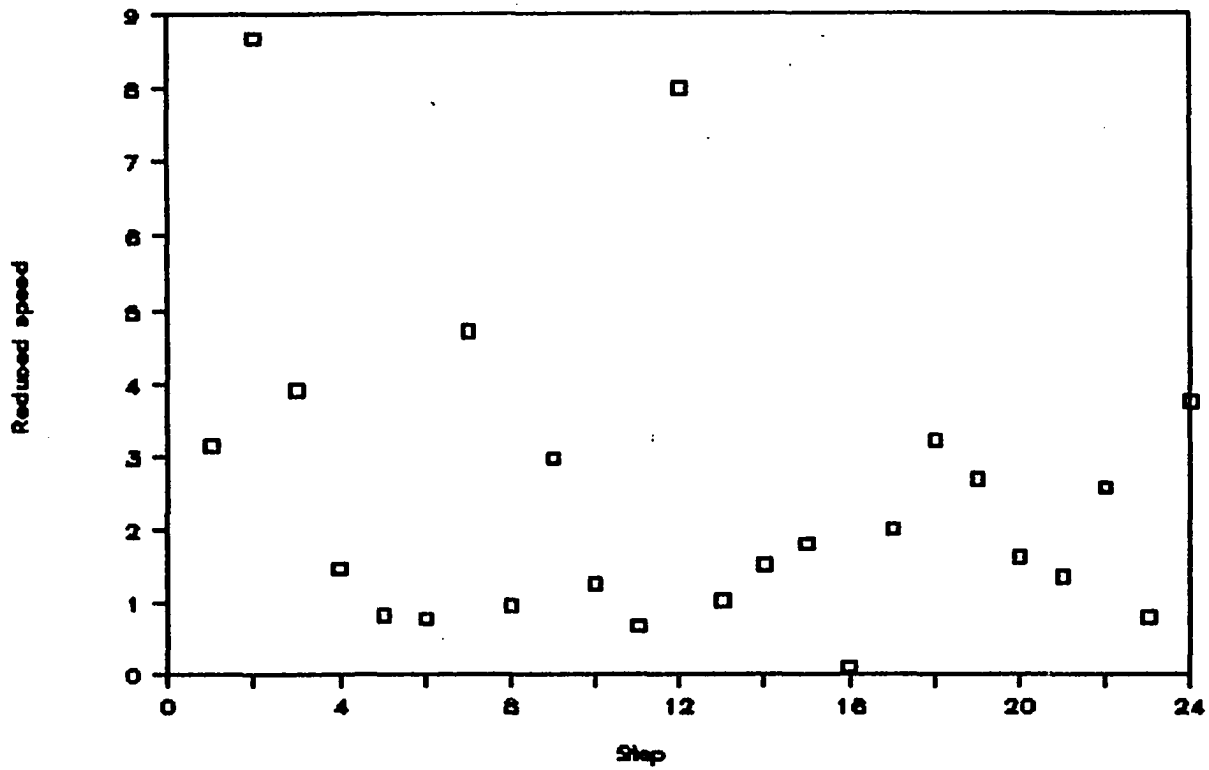


Figure 68. Reduced speeds for the length of the apical process in R.bergonii in DSDP site 573.

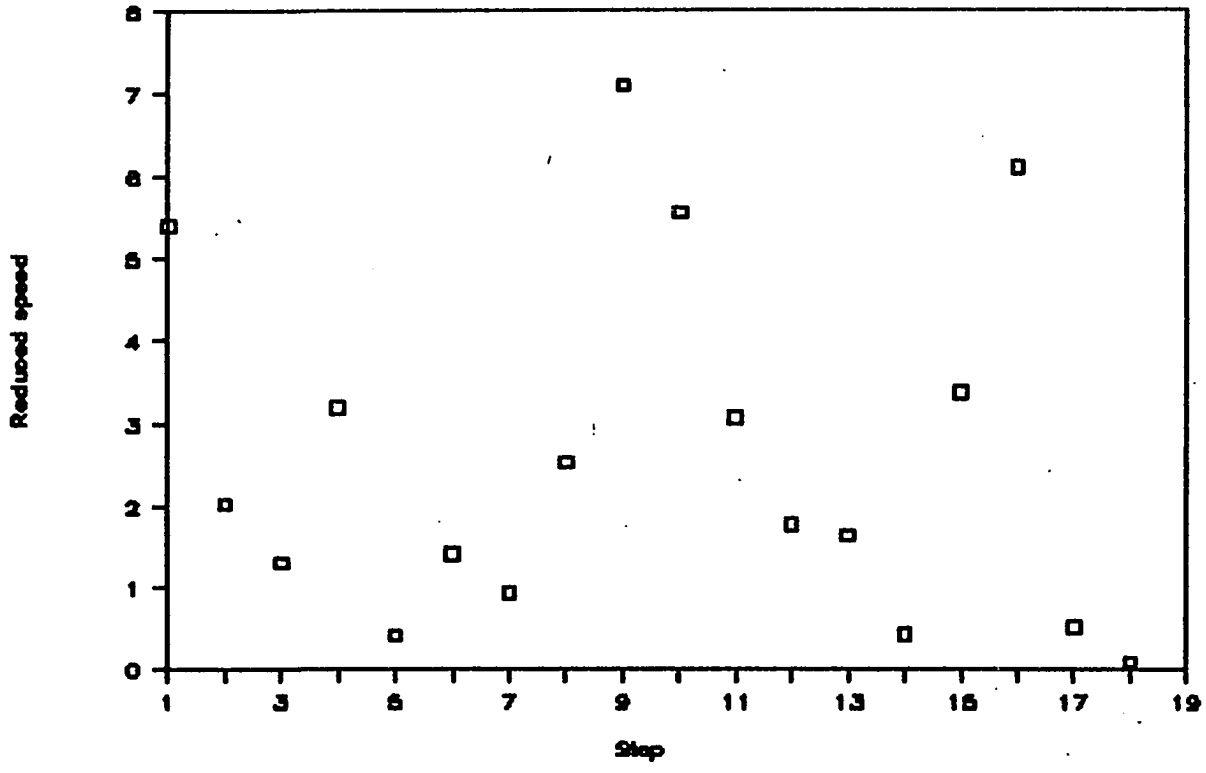


Figure 69. Reduced speeds for the length of the apical process in R.bergonii in site RC12-66.

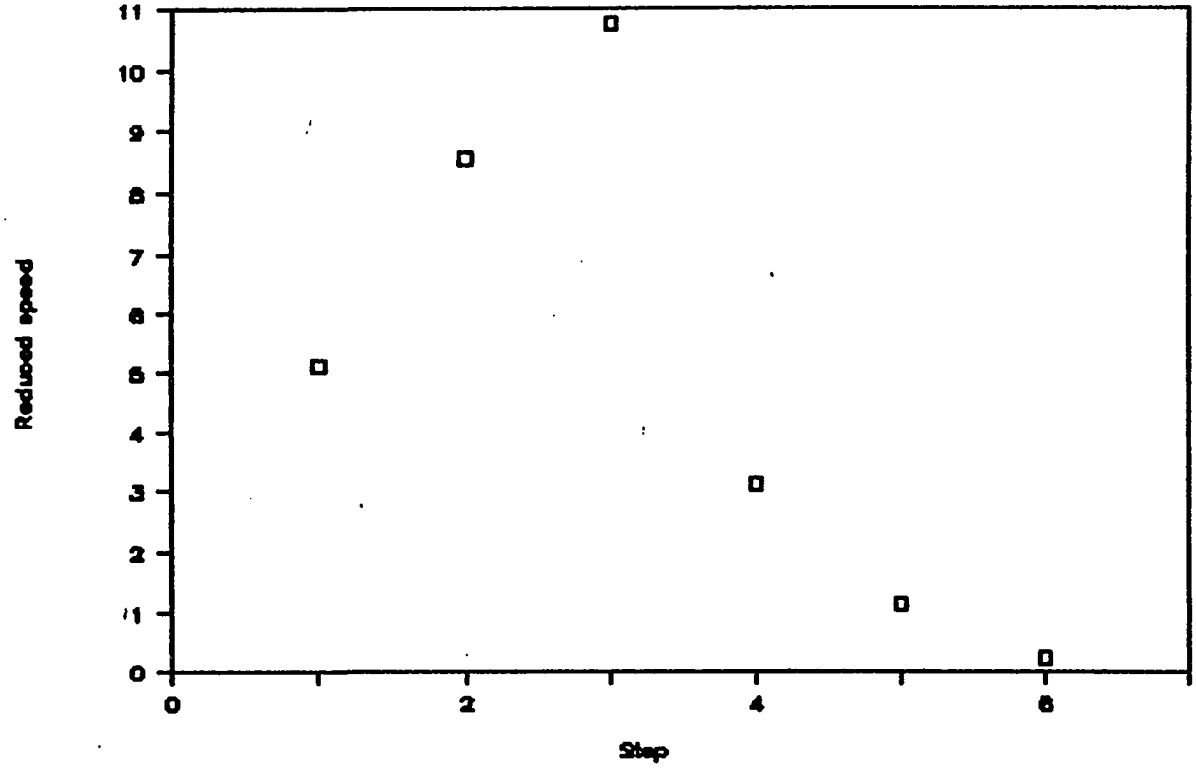


Figure 70. Reduced speeds for the length of the apical process in R.sigmoida in DSDP site 504.

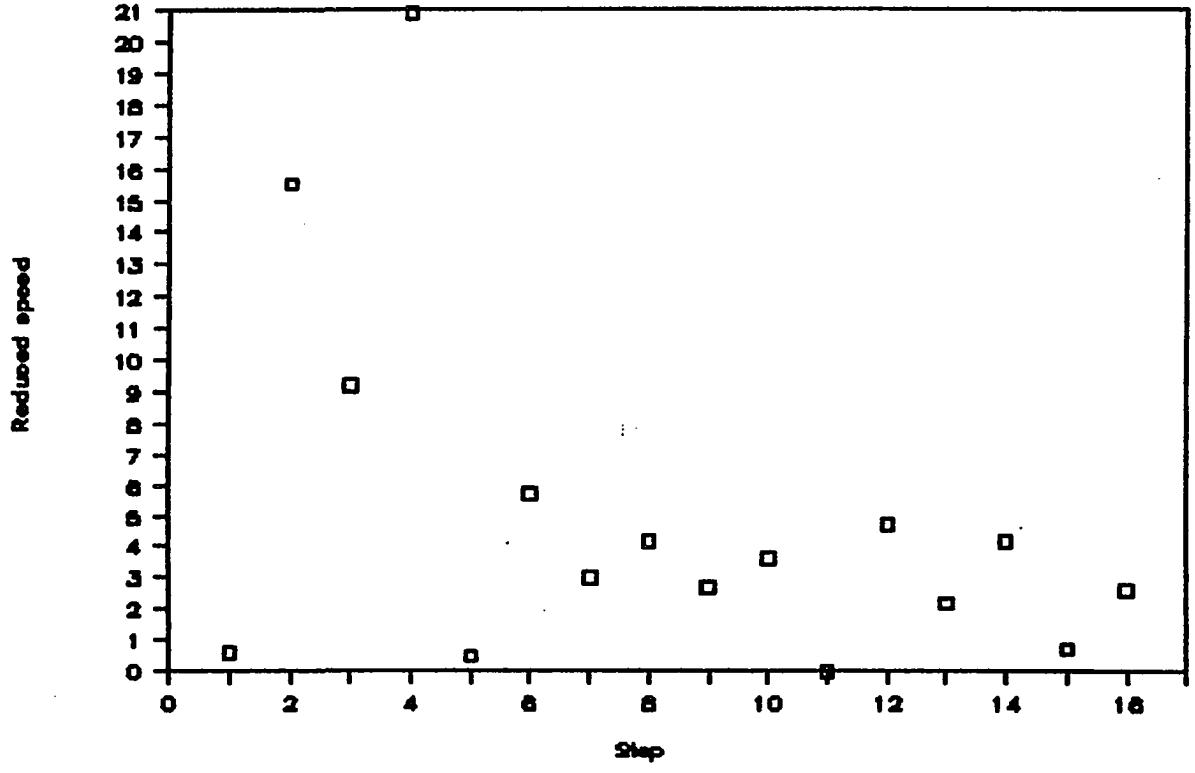


Figure 71. Reduced speeds for the length of the apical process in R.sigmoida in DSDP site 157.

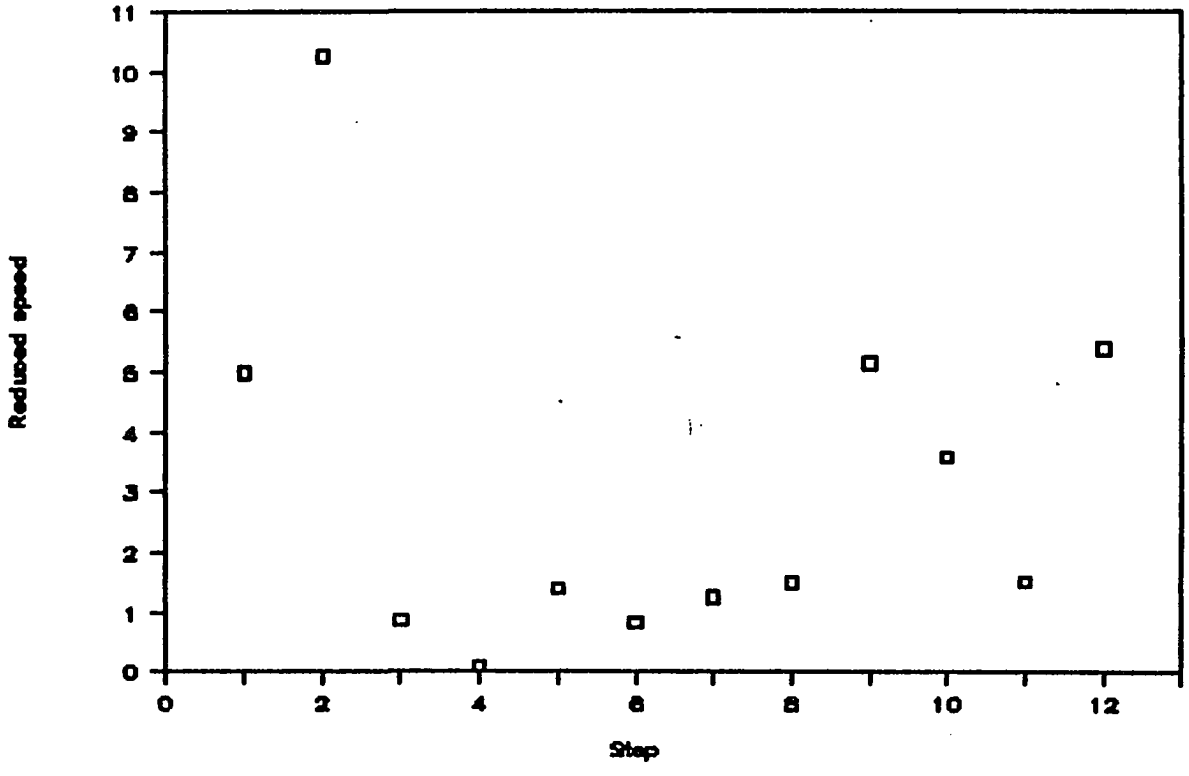


Figure 72. Reduced speeds for the length of the apical process in R.bergonii in the Indian Ocean sites.

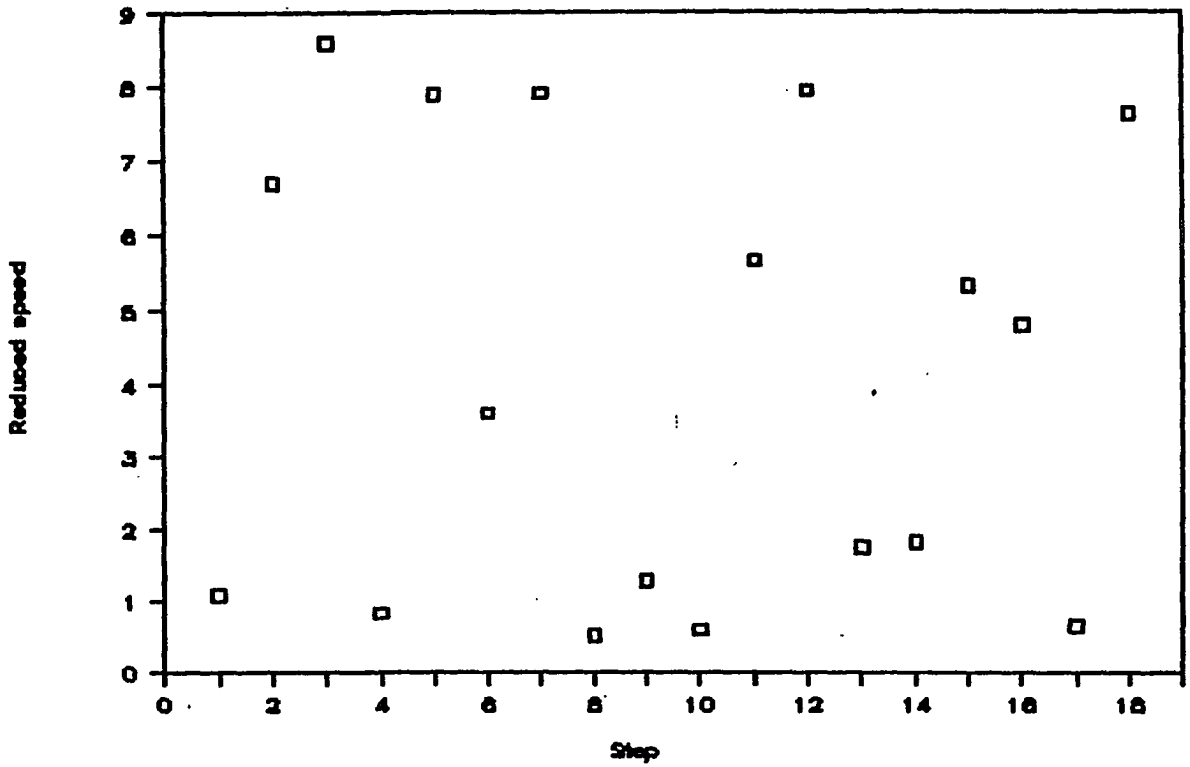


Figure 73. Reduced speeds for the length of the apical process in R.praebergonii in DSDP site 572c.

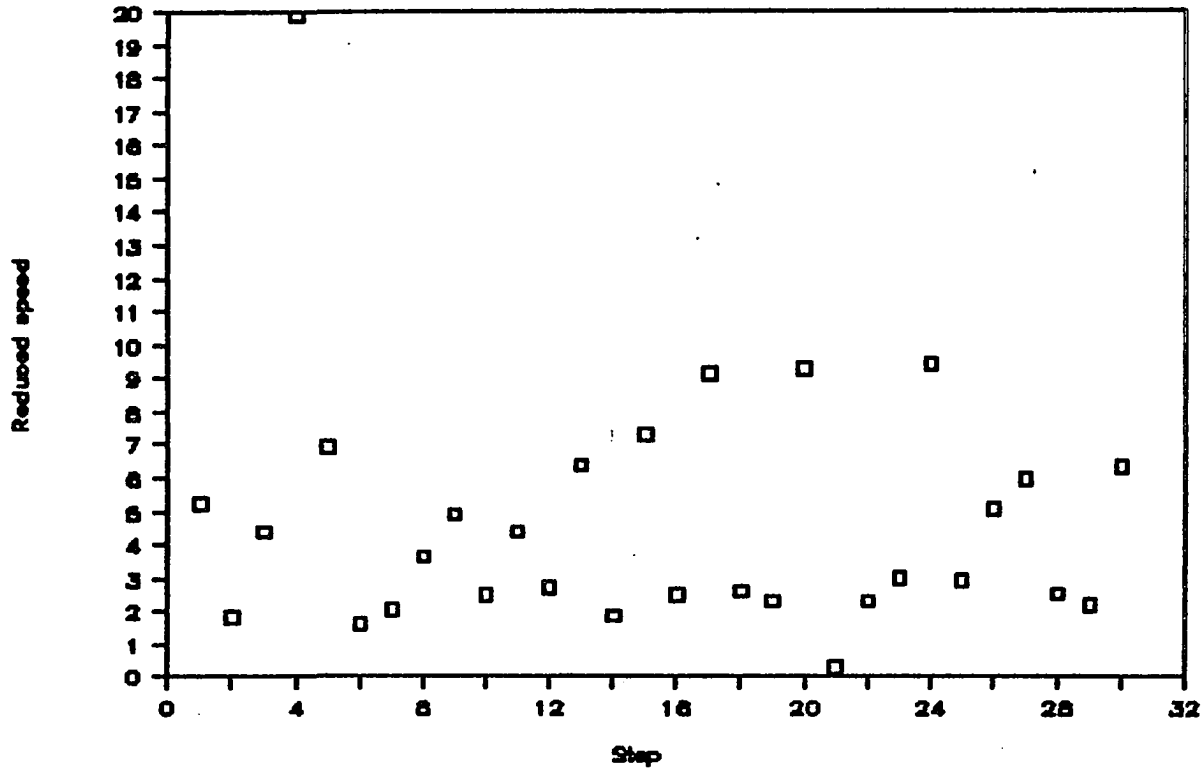


Figure 74. Reduced speeds for the length of the apical process in R.praebergonii in DSDP site 157.

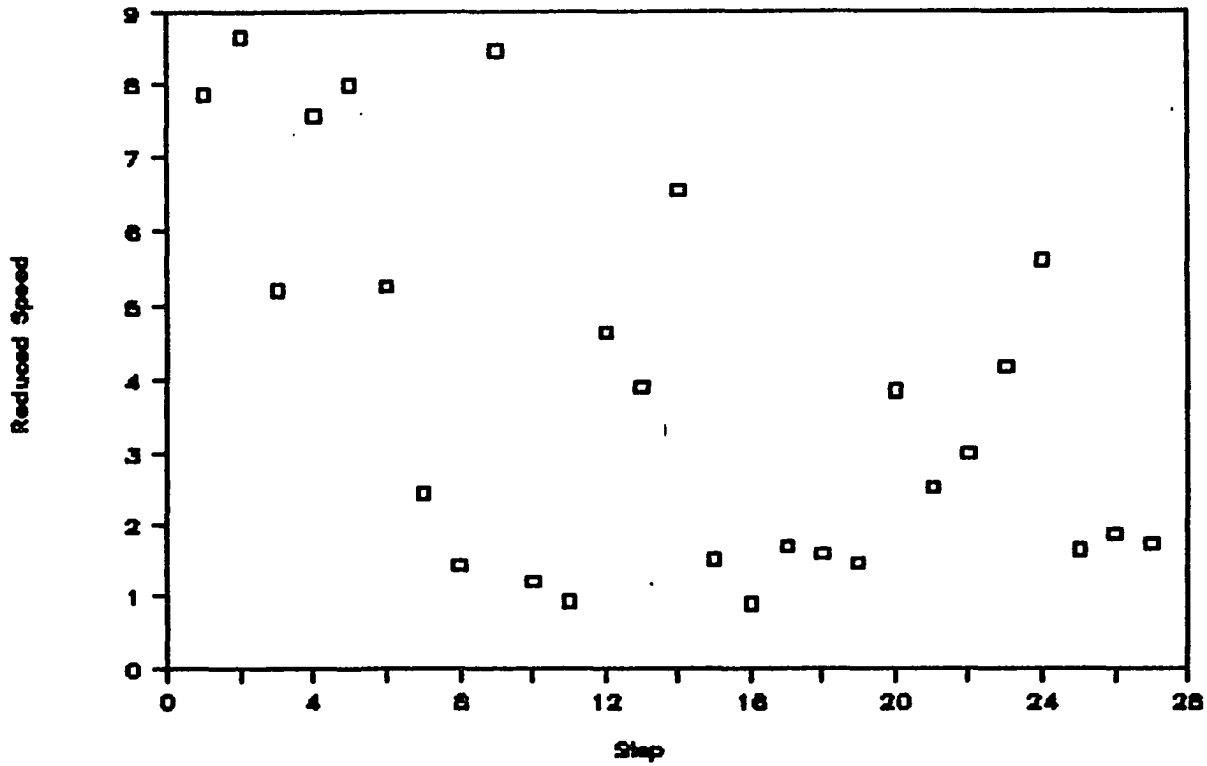


Figure 75. Reduced speeds for the length of the apical process in R.praebergonii in DSDP site 573.

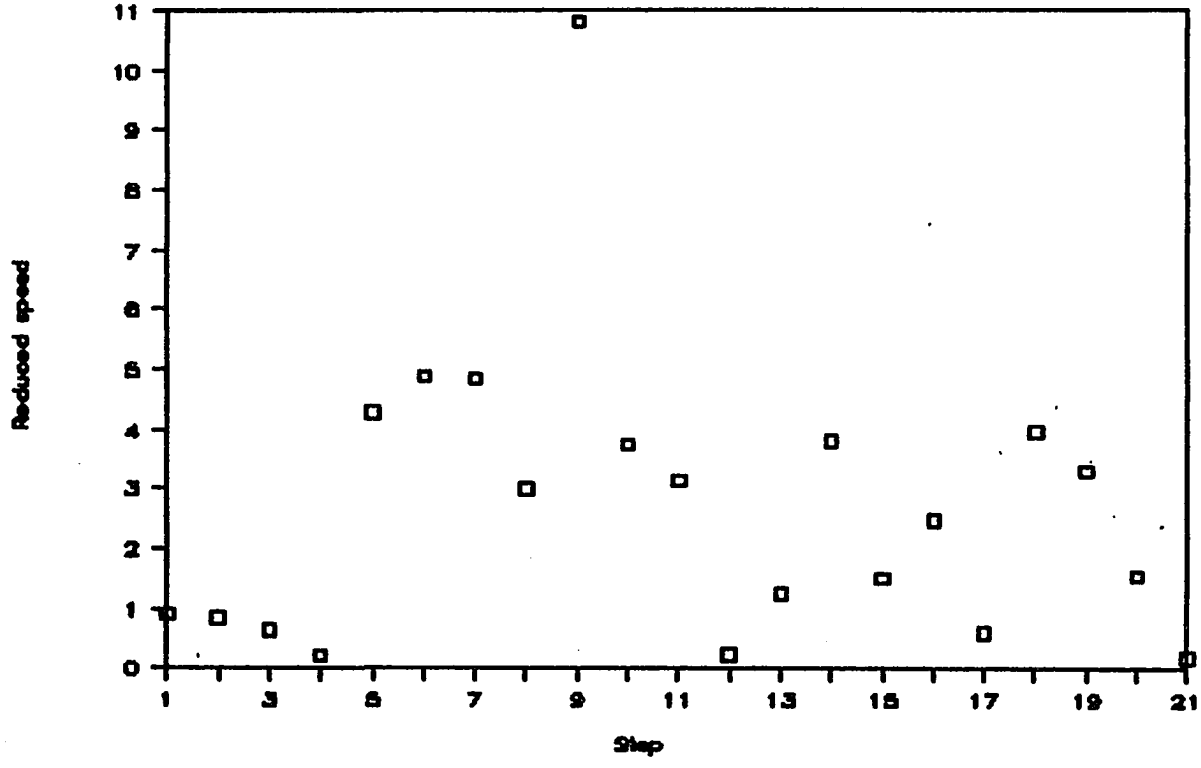


Figure 76. Reduced speeds for the length of the apical process in R.praebergonii in the Indian Ocean sites.

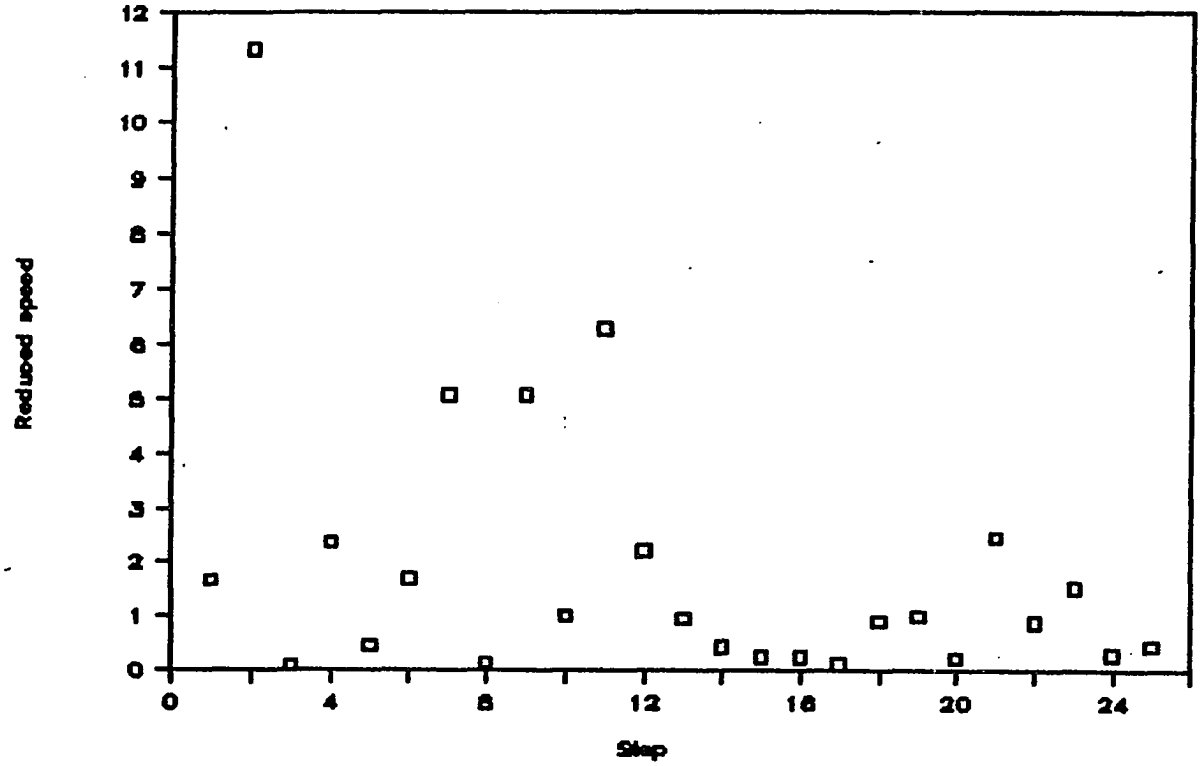


Figure 77. Reduced speeds for the length of the apical process in R.praebergonii in site RC12-66.

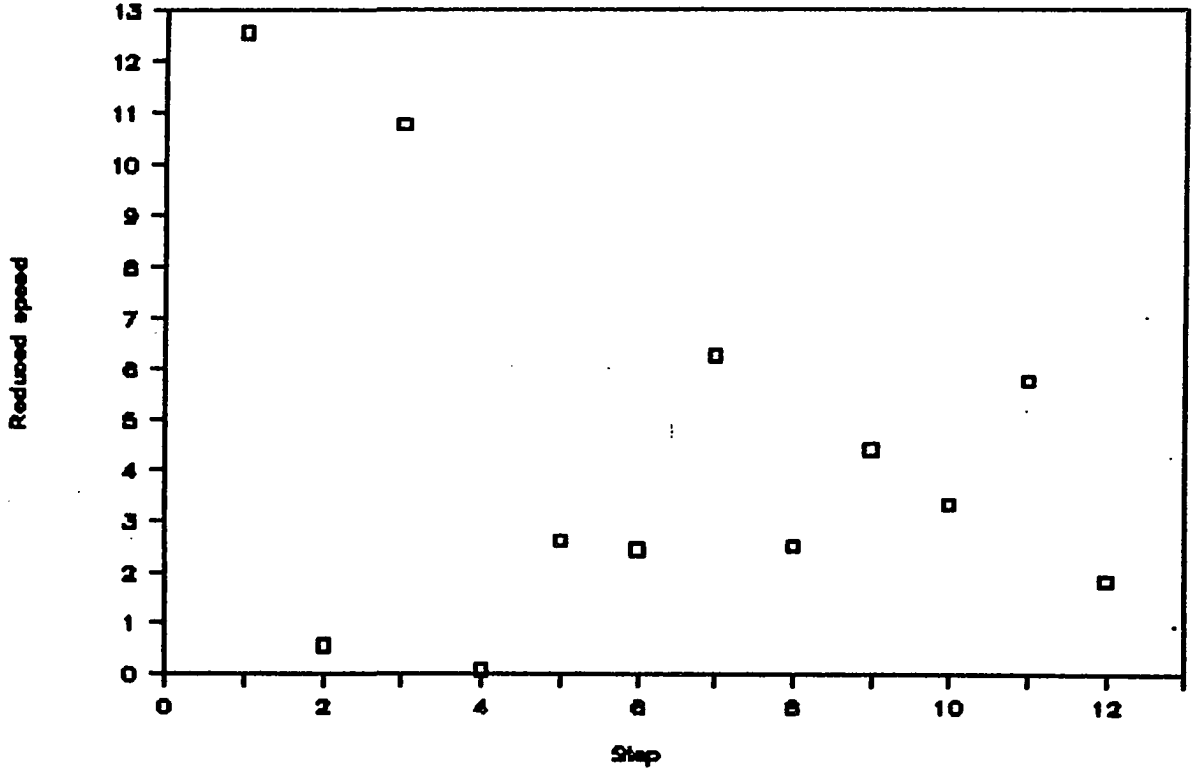


Figure 78. Reduced speeds for the length of the apical process in R.praebergonii in site V28-179.

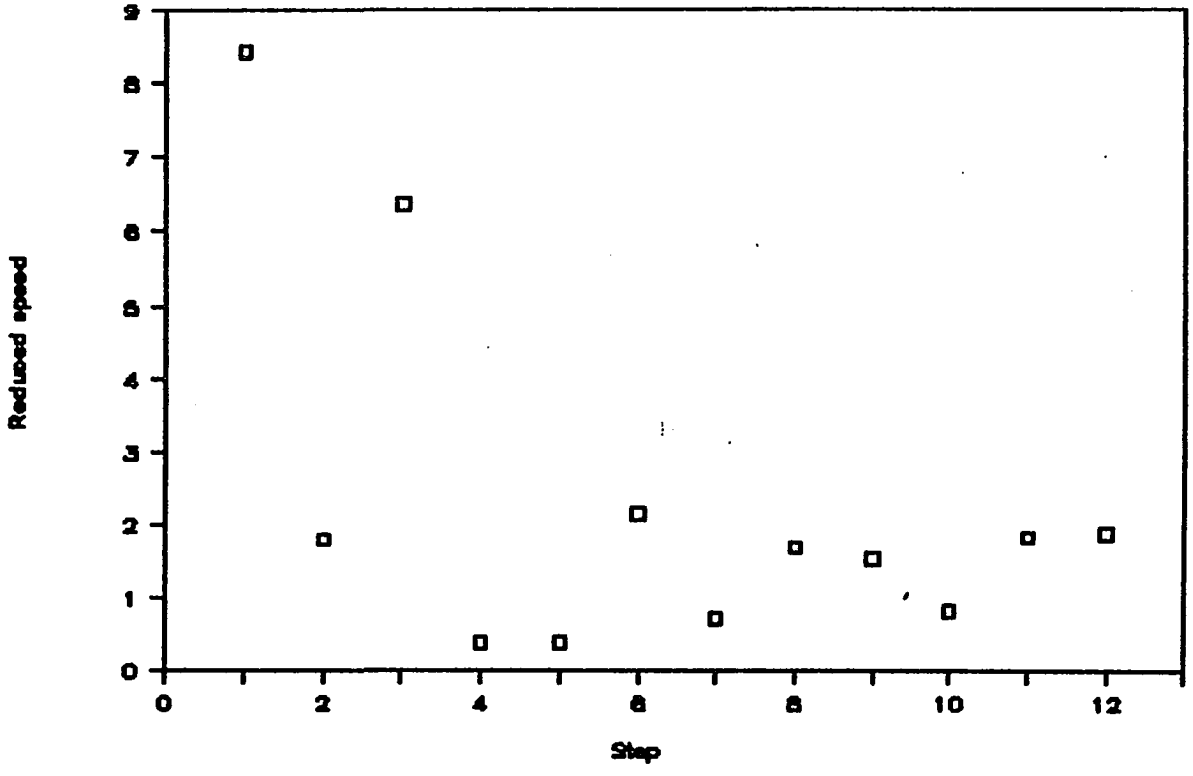


Figure 79. Reduced speeds for the height of the hyaline area in R.praebergonii in site V28-179.

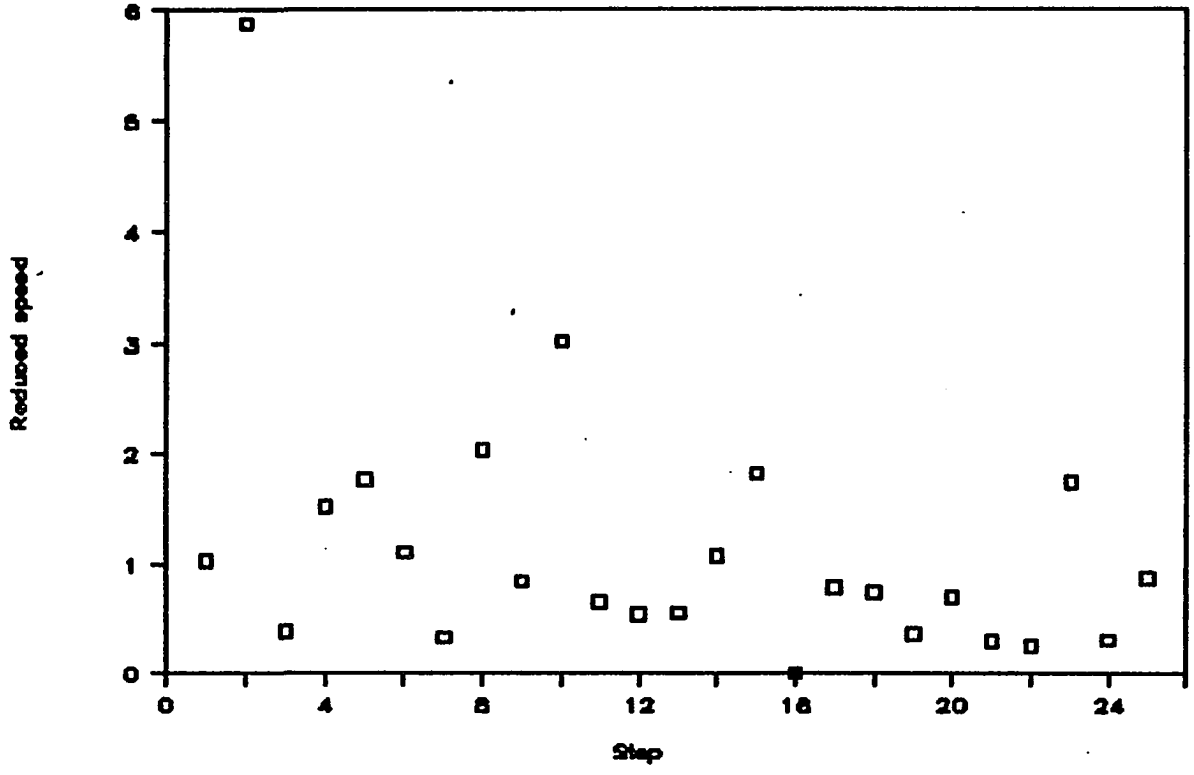


Figure 80. Reduced speeds for the height of the hyaline area in R.praebergonii in site RC12-66.

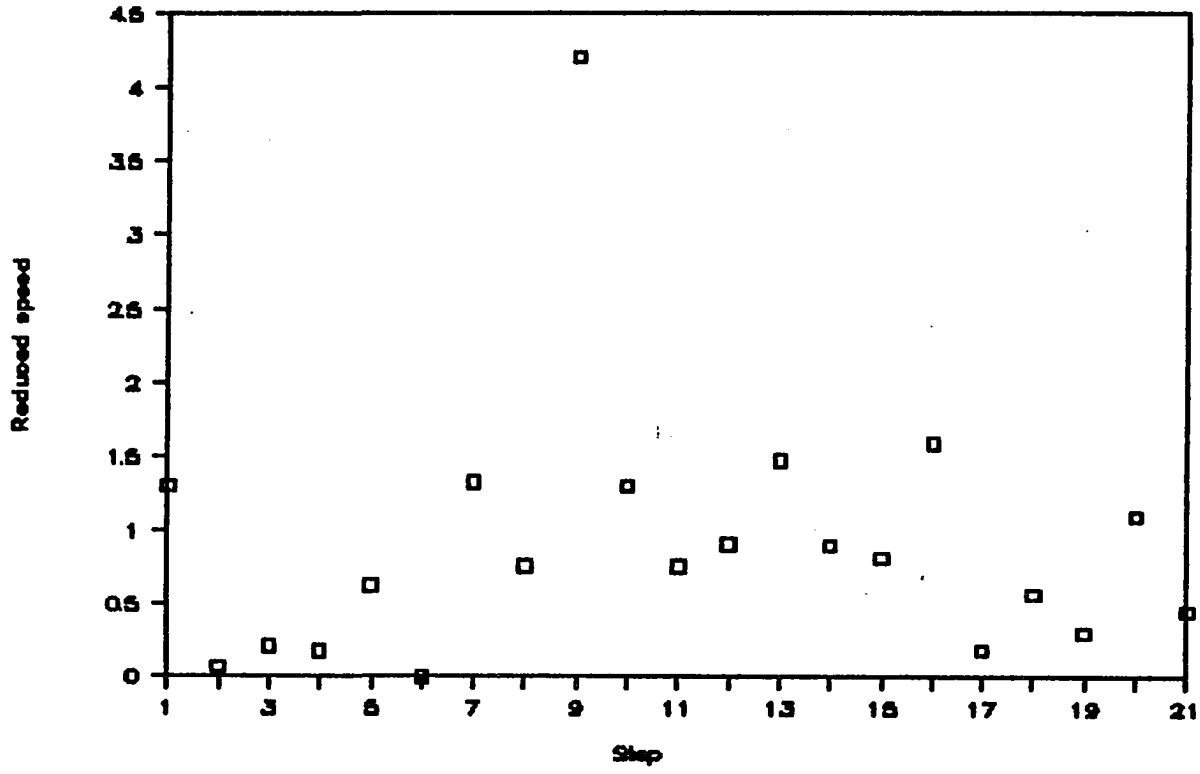


Figure 81. Reduced speeds for the height of the hyaline area in R.praebergonii in the Indian Ocean sites.

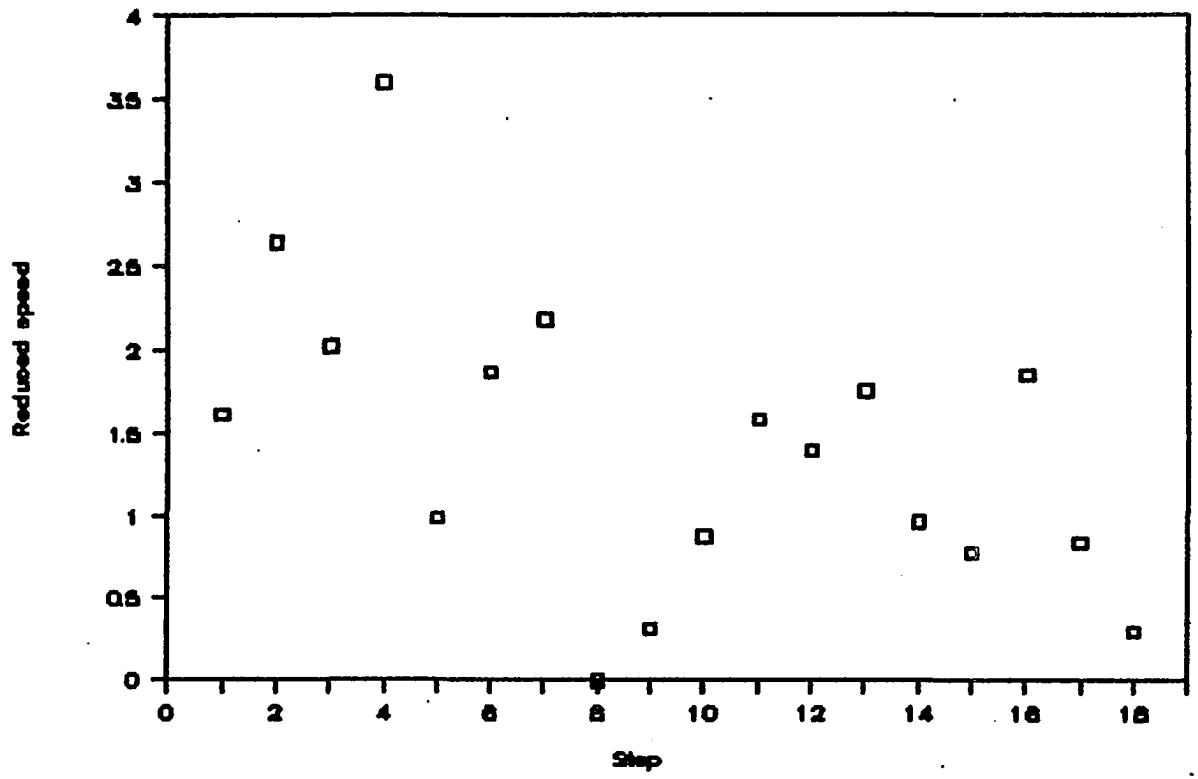


Figure 82. Reduced speeds for the height of the hyaline area in R.praebergonii in DSDP site 572c.

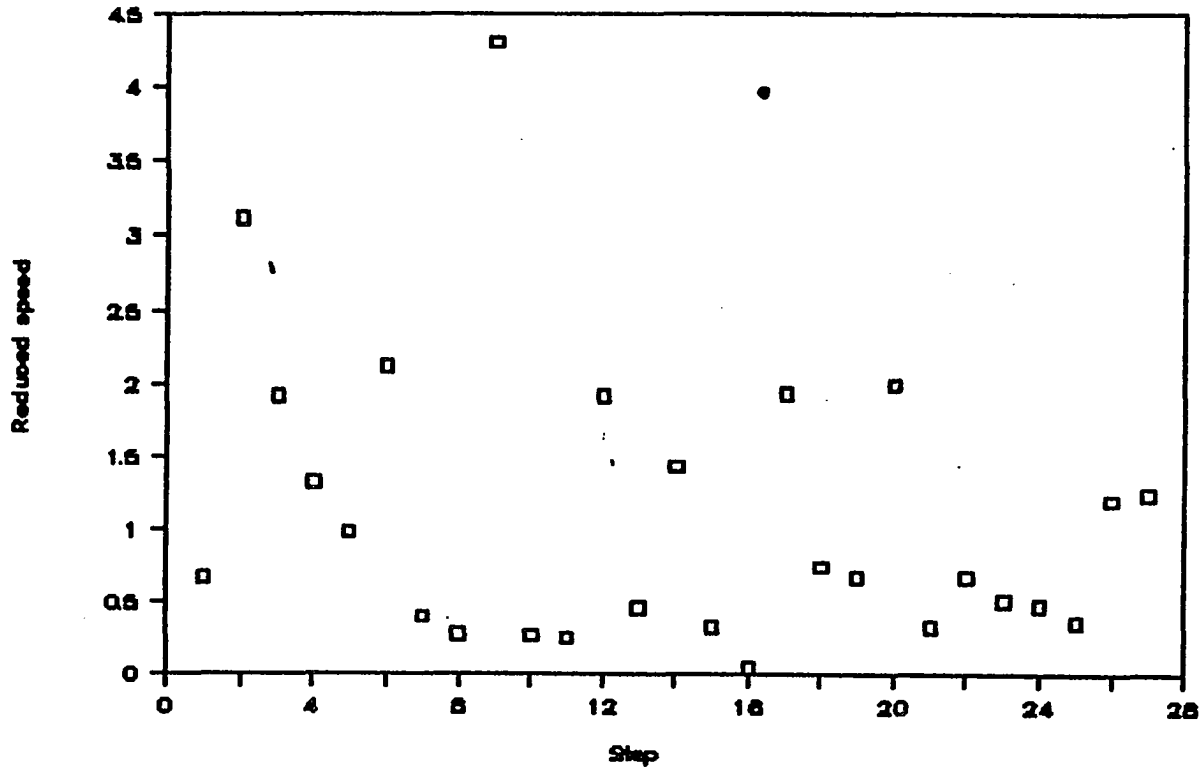


Figure 83. Reduced speeds for the height of the hyaline area in R.praebergonii in DSDP site 573.

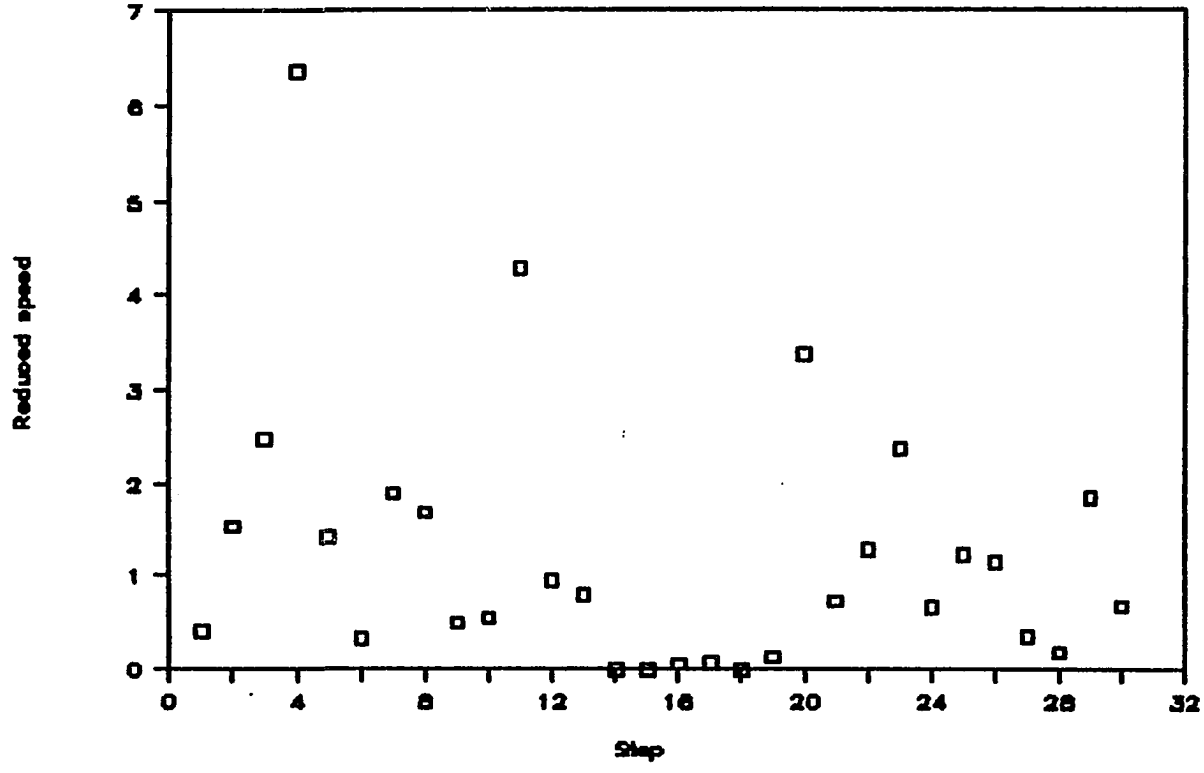


Fig 84. Reduced speeds for the height of the hyaline area in R.praebergonii in DSDP site 157.

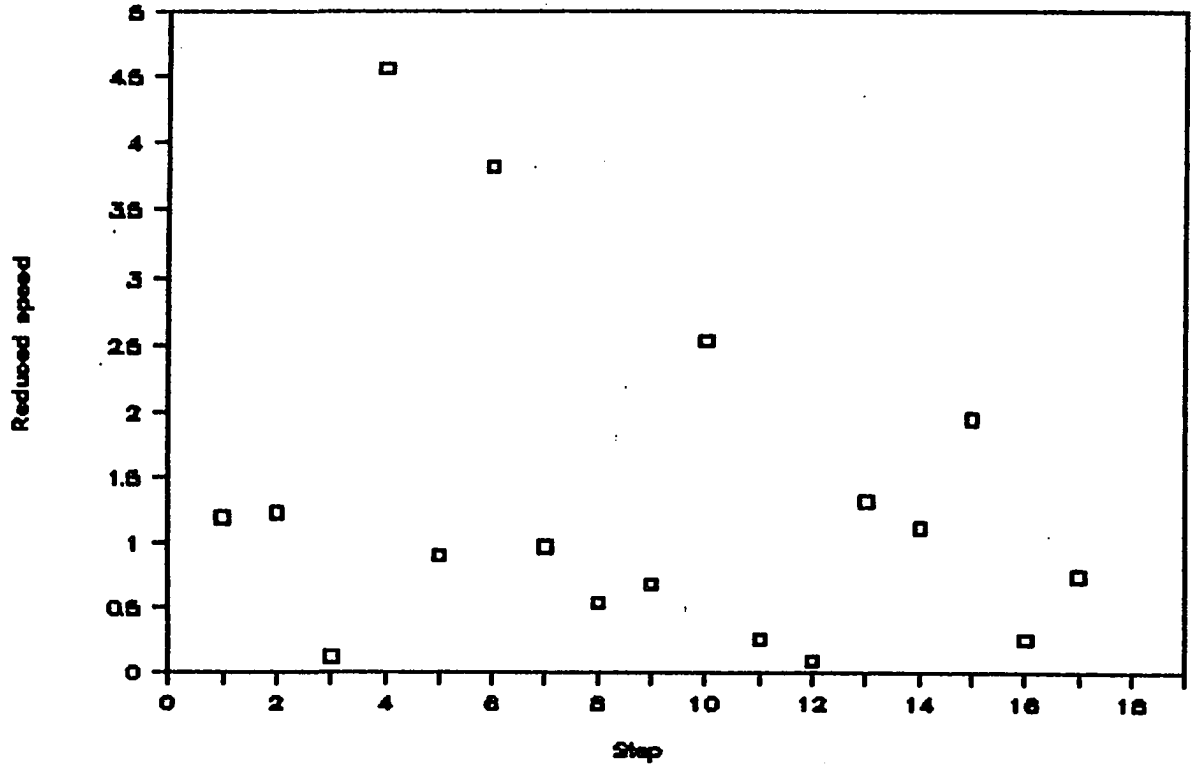


Figure 85. Reduced speeds for the height of the hyaline area in R.sigmoida in DSDP site 157.

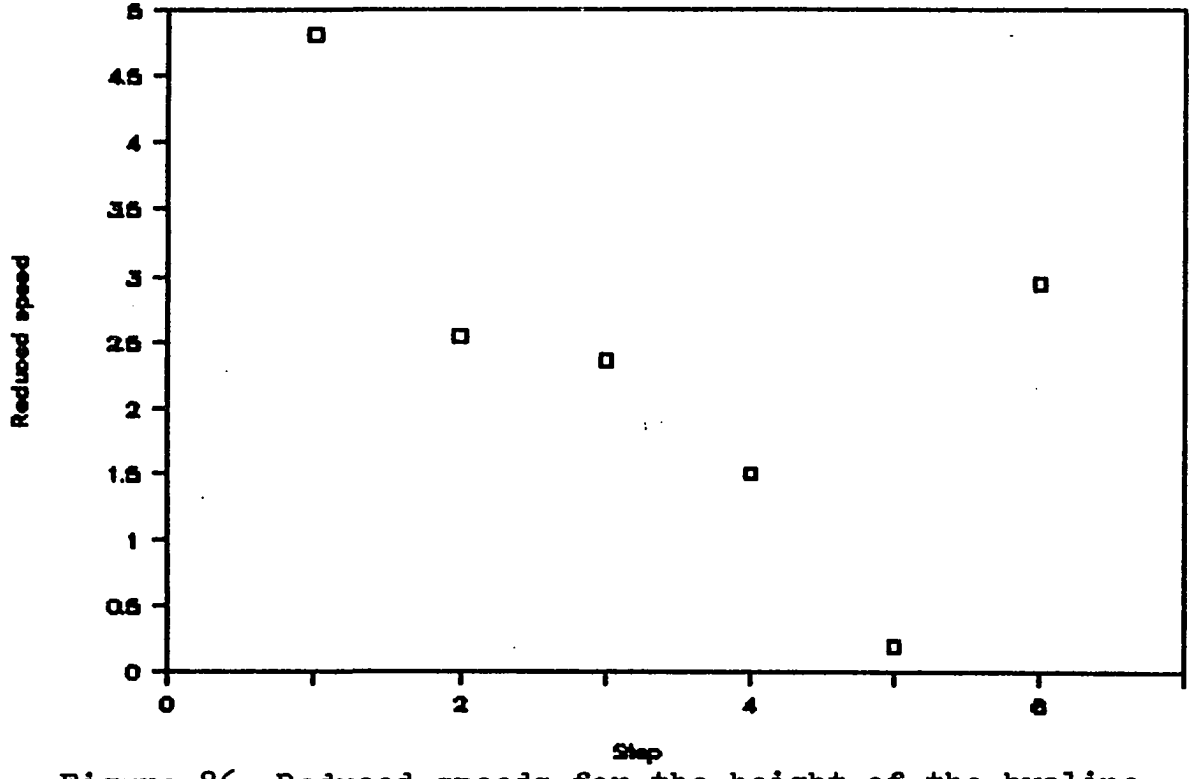


Figure 86. Reduced speeds for the height of the hyaline area in R.sigmoida in DSDP site 504.

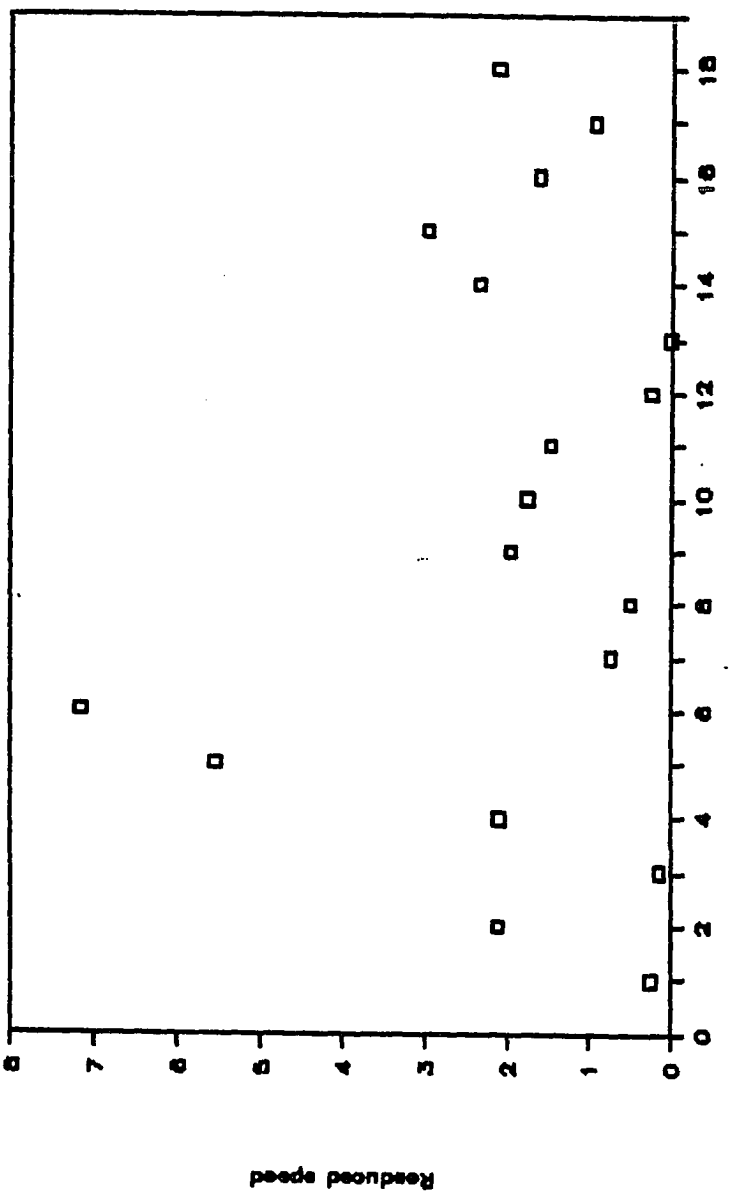


Figure 87. Reduced speeds for the height of the hyaline area in R.bergonii in site RC12-66.

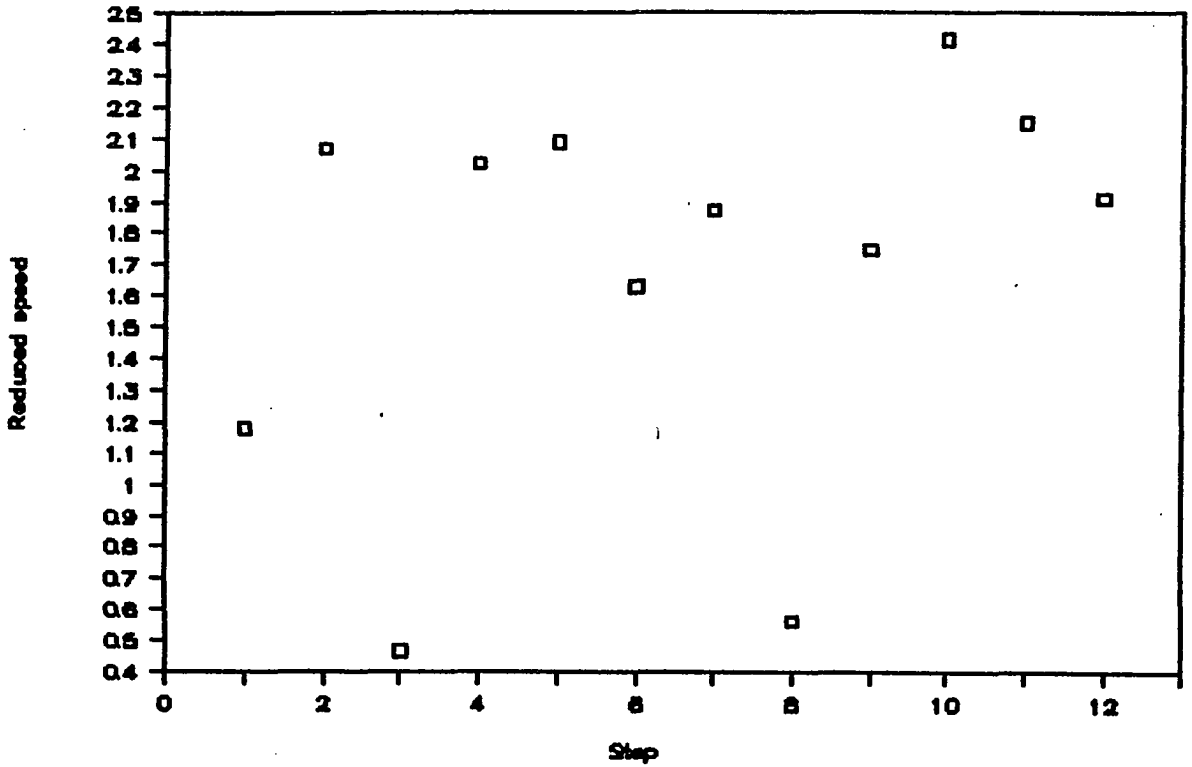


Figure 88. Reduced speeds for the height of the hyaline area in R.bergonii in the Indian Ocean sites.

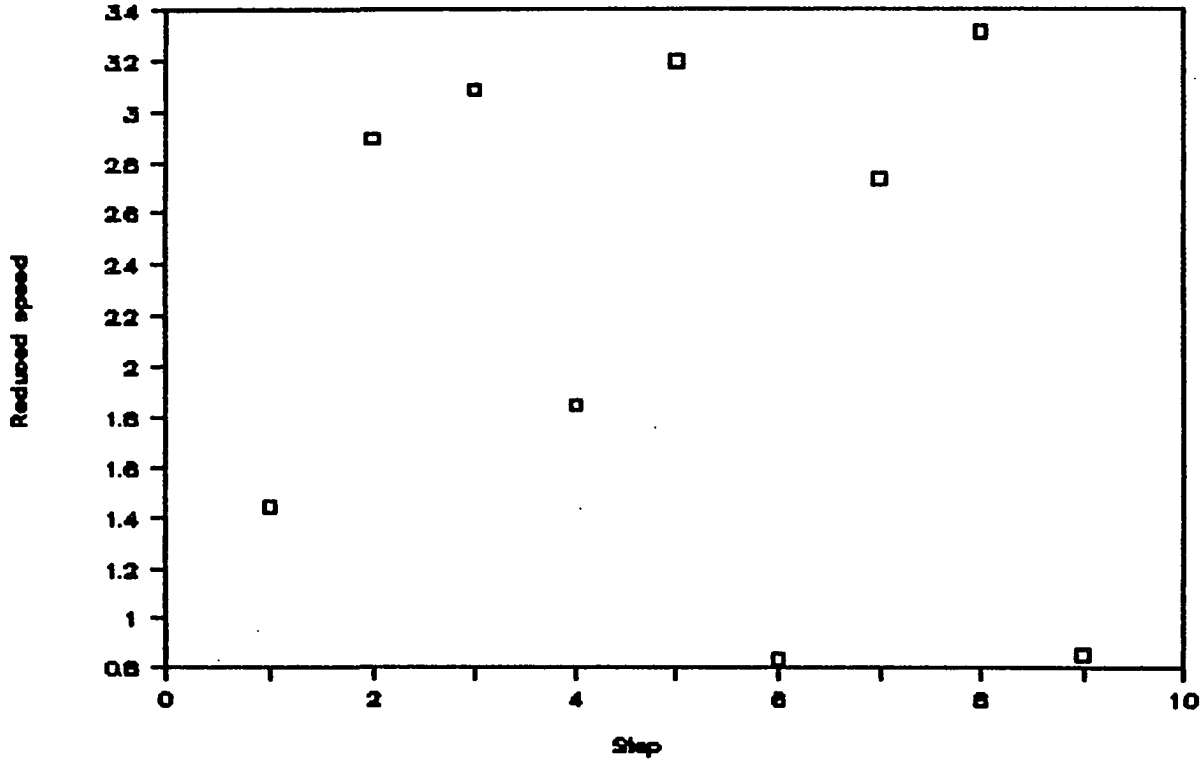


Figure 89. Reduced speeds for the height of the hyaline area in R.bergonii in DSDP site 504.

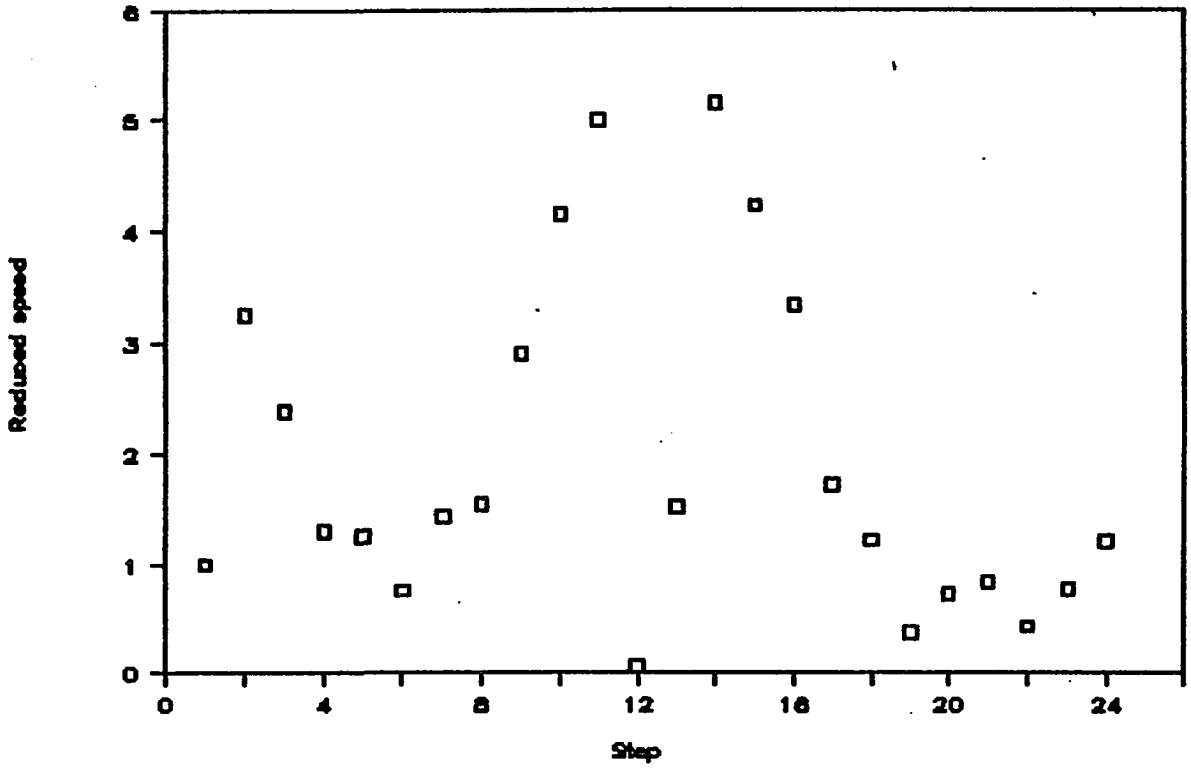


Figure 90. Reduced speeds for the height of the hyaline area in R.bergonii in DSDP site 573.

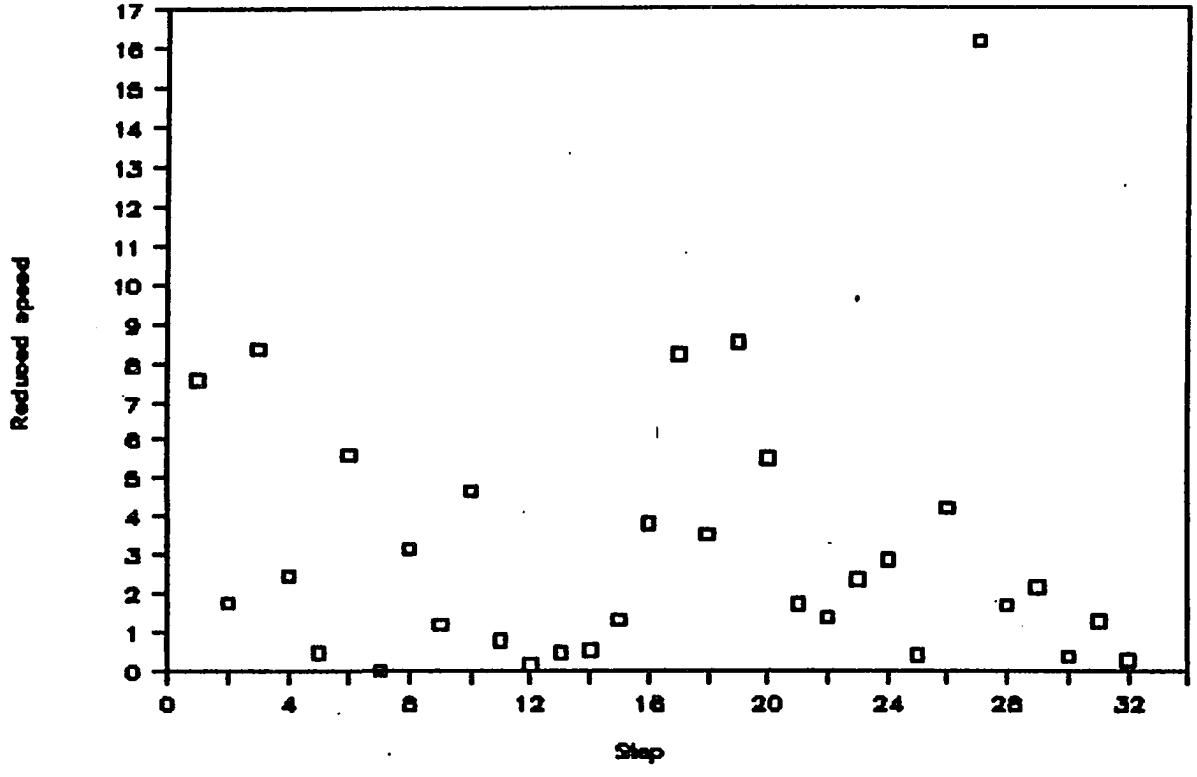


Figure 91. Reduced speeds for the height of the hyaline area in R.bergonii in DSDP site 157.

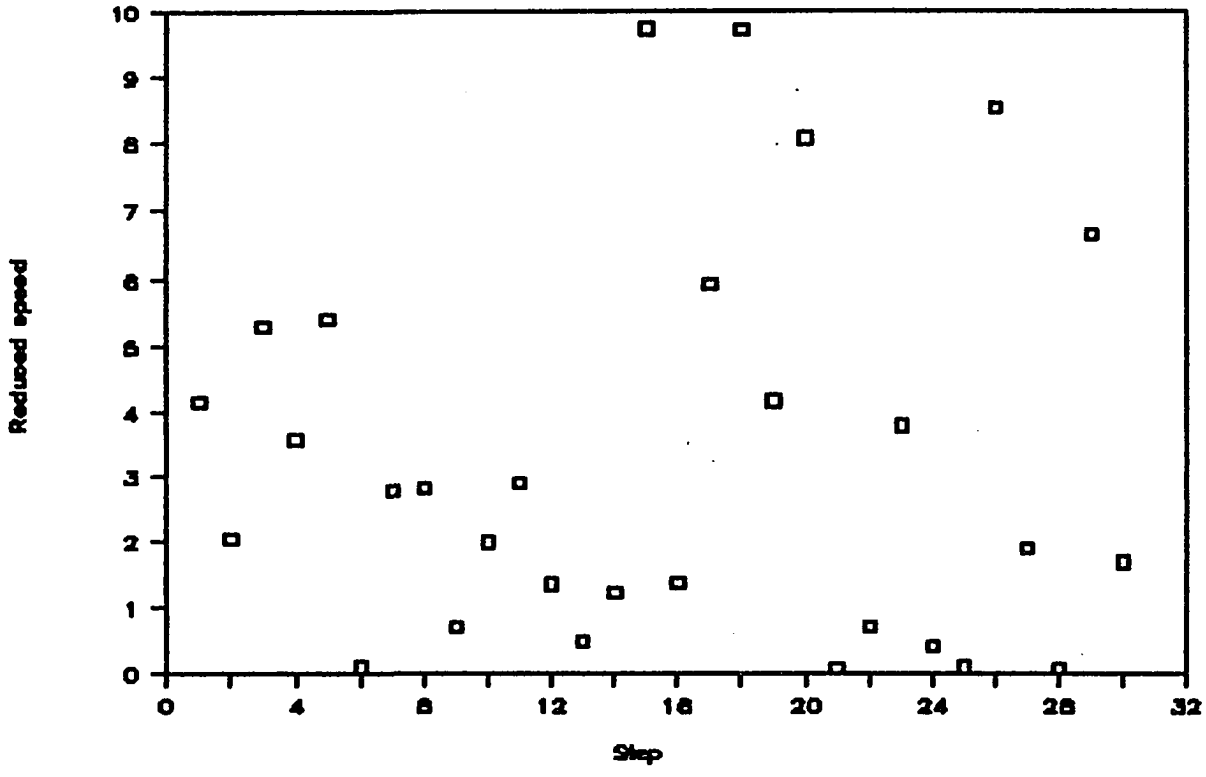


Figure 92. Reduced speeds for the width of the valve in R.praebergonii in DSDP site 157.

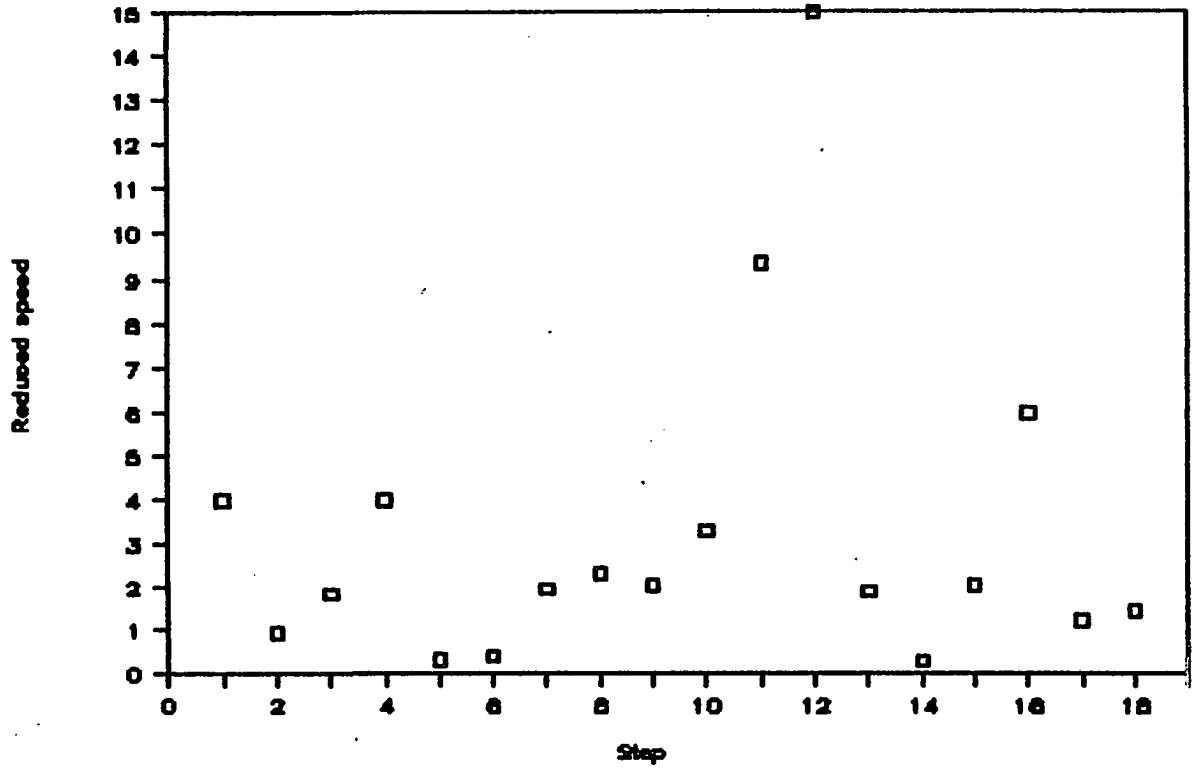


Figure 93. Reduced speeds for the width of the valve in R.praebergonii in DSDP site 572c.

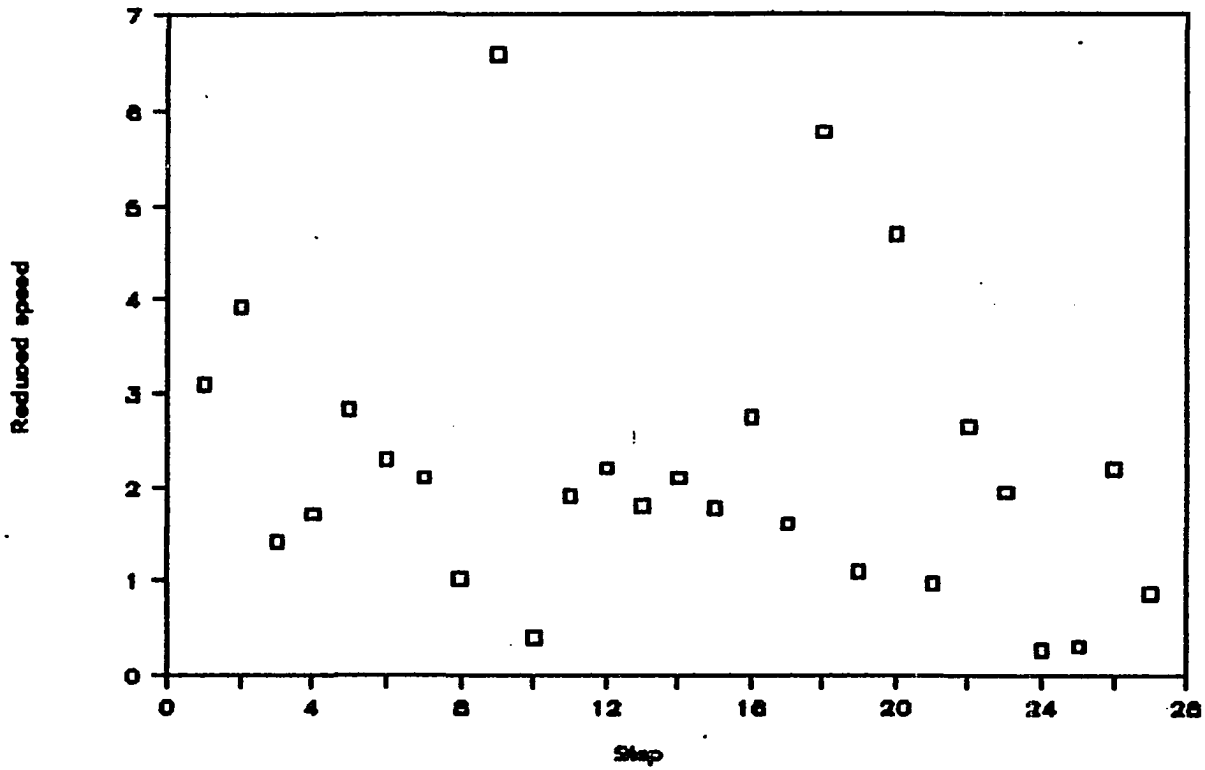


Figure 94. Reduced speeds for the width of the valve in R.praebergonii in DSDP site 573.

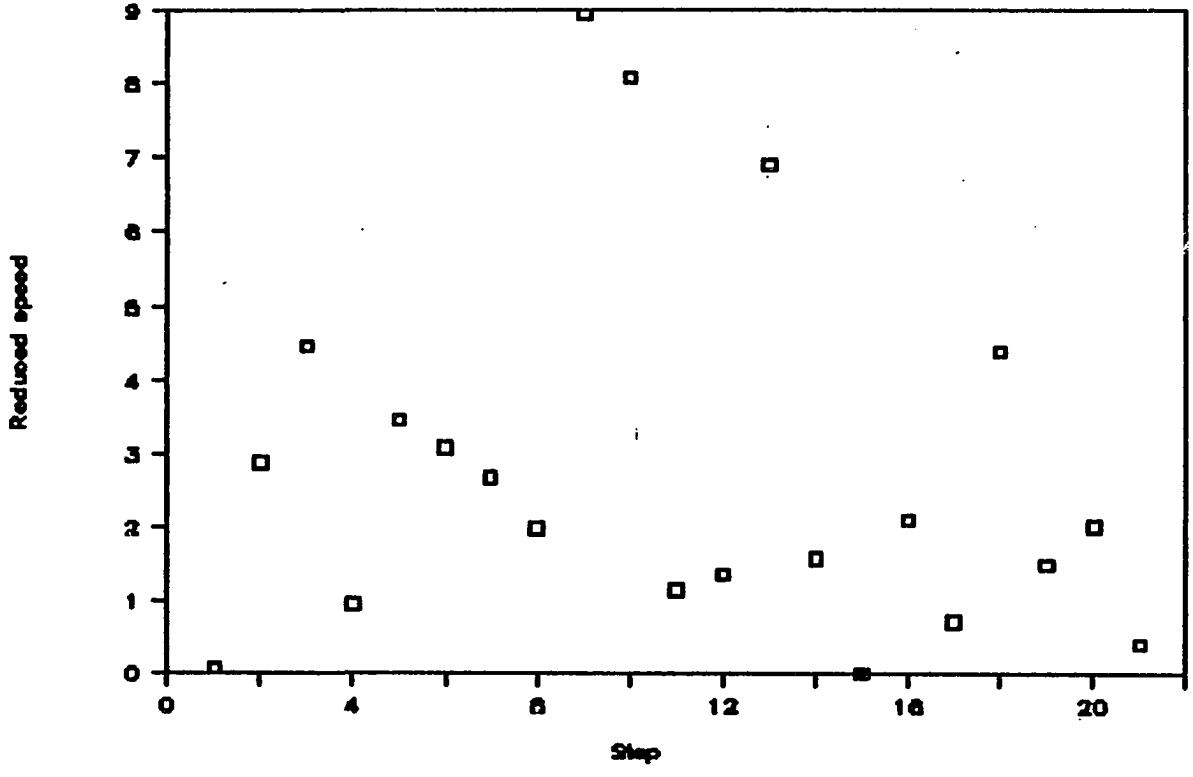


Figure 95. Reduced speeds for the width of the valve in R.praebergonii in the Indian Ocean sites.

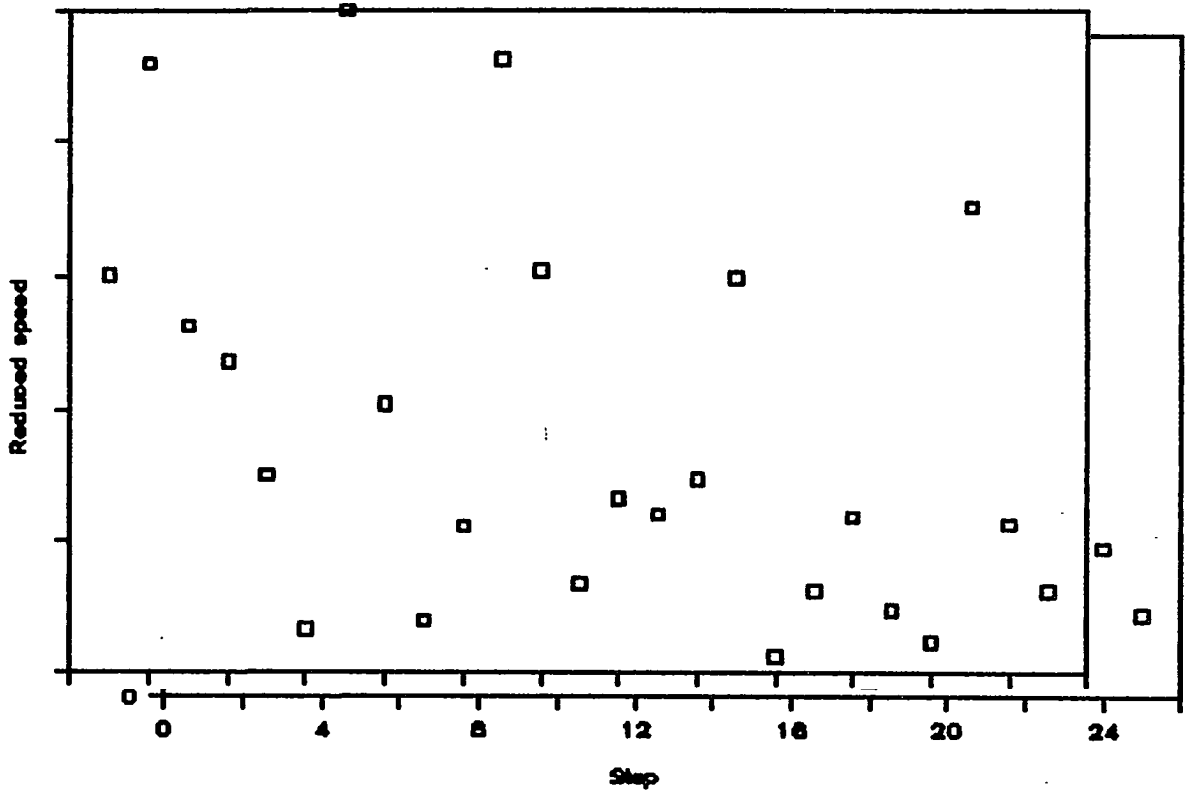


Figure 96. Reduced speeds for the width of the valve in R.praebergonii in site RC12-66.

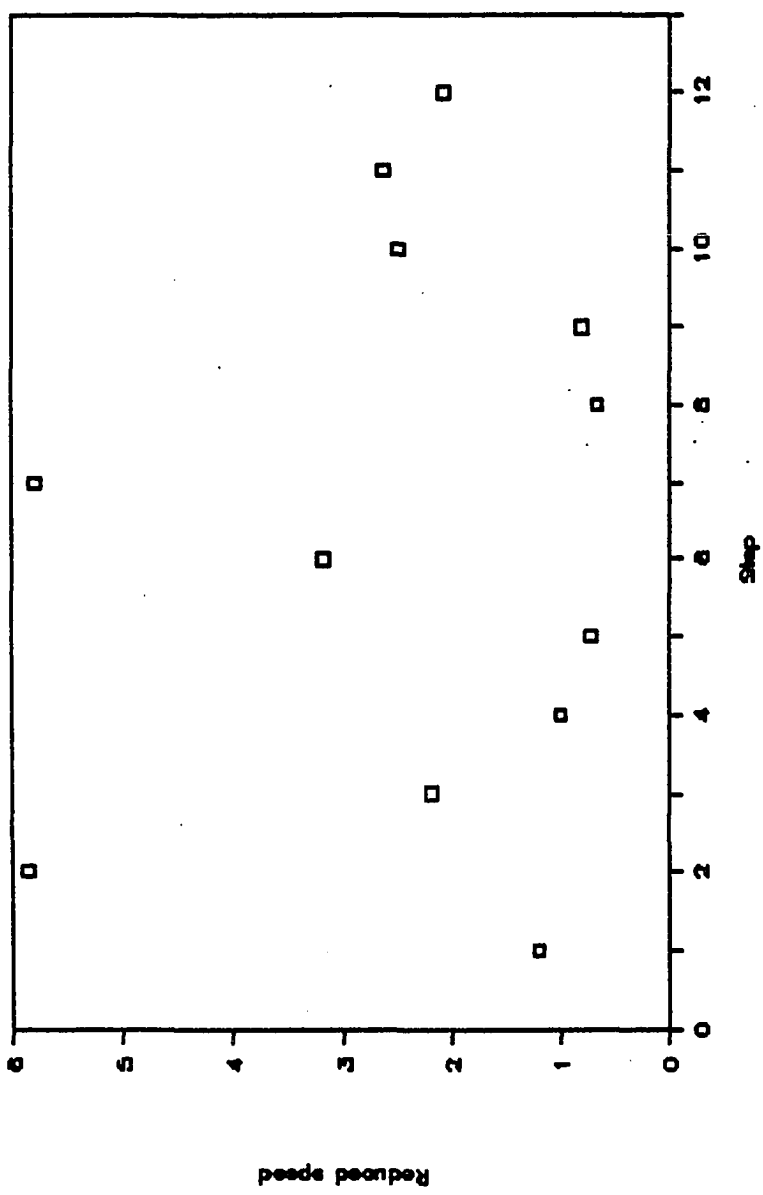


Figure 97. Reduced speeds for the width of the valve in R.praebergonii in site V28-179.

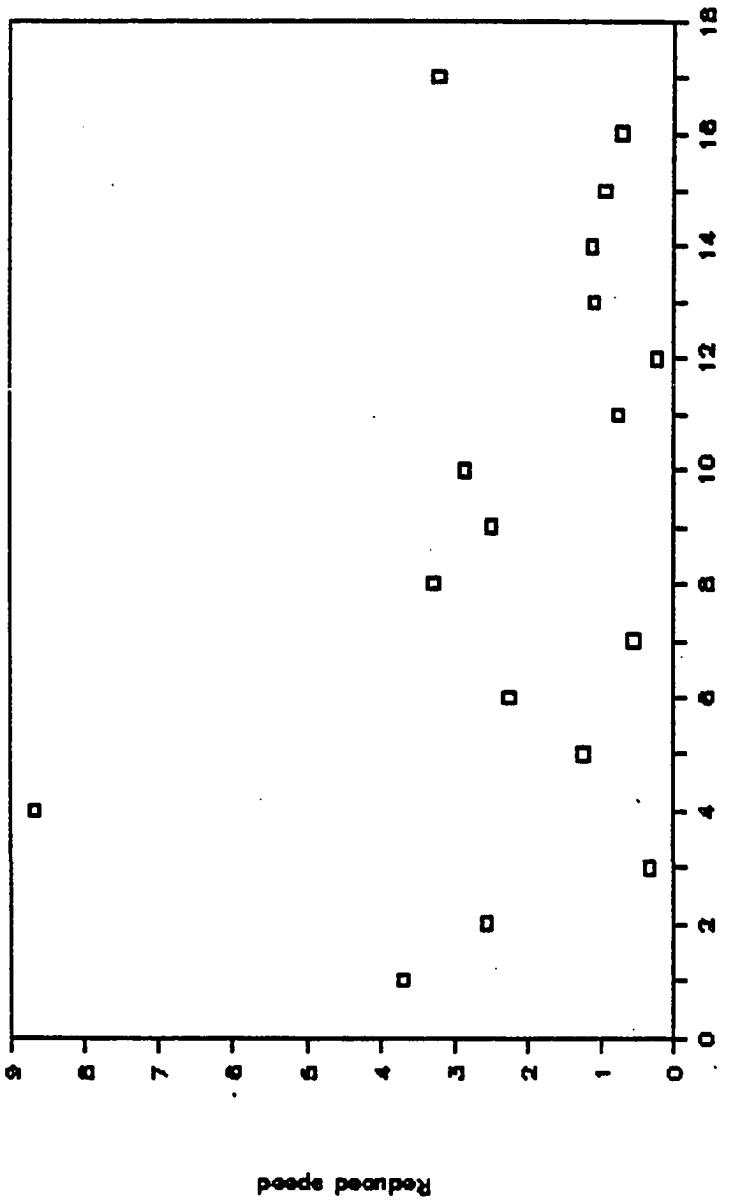


Figure 98. Reduced speeds for the width of the valve in R.sigmoida in DSDP site 157.

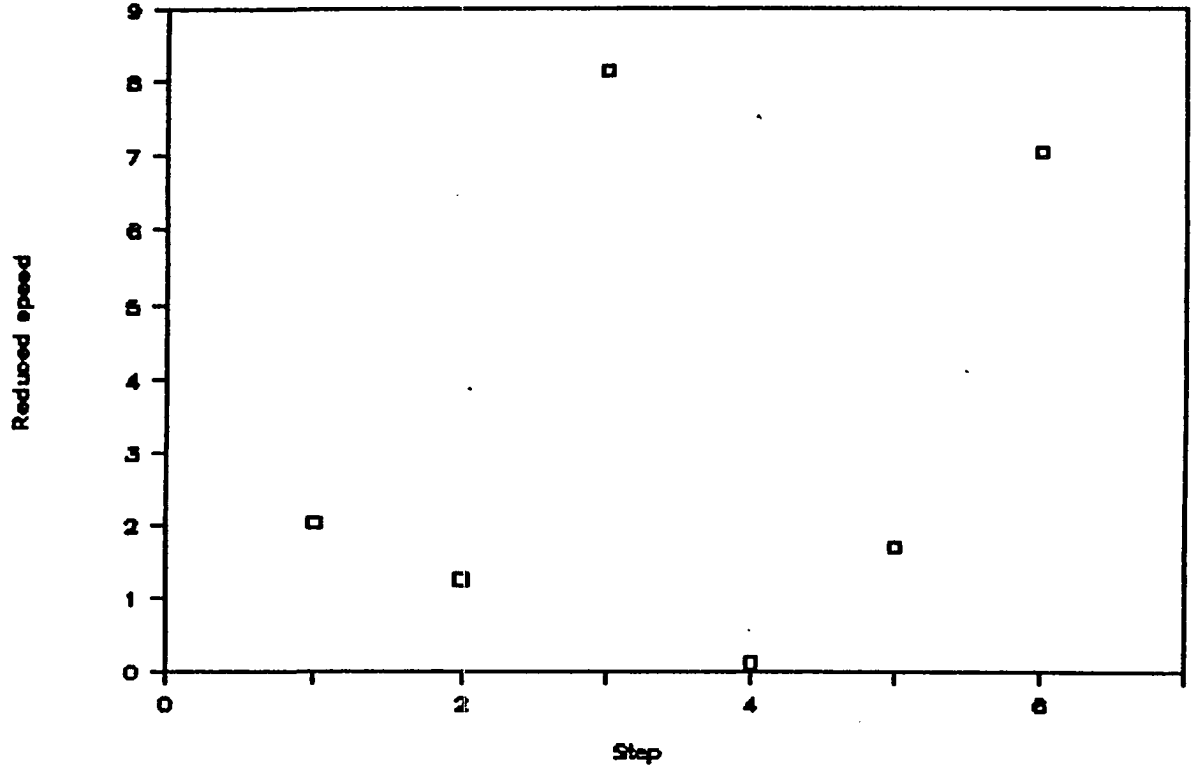


Figure 99. Reduced speeds for the width of the valve in R. sigmoida in DSDP site 504.

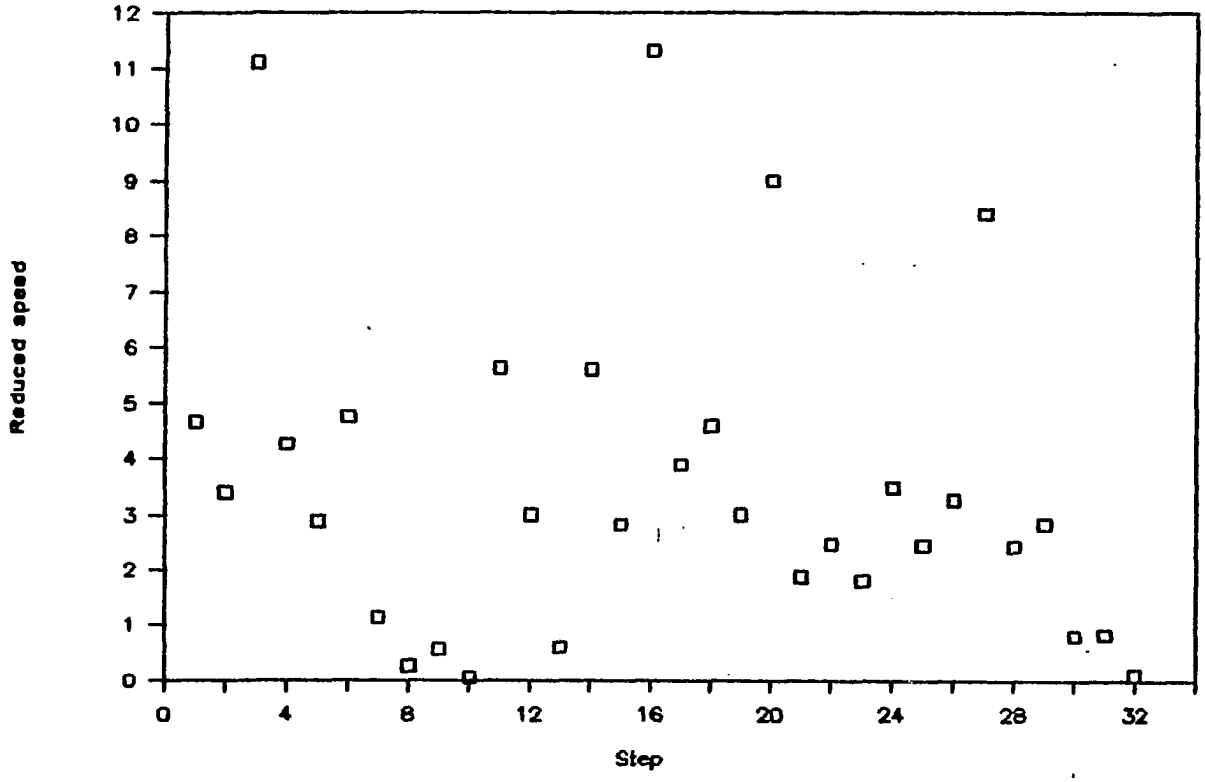


Figure 100. Reduced speeds for the width of the valve in R.bergonii in DSDP site 157.

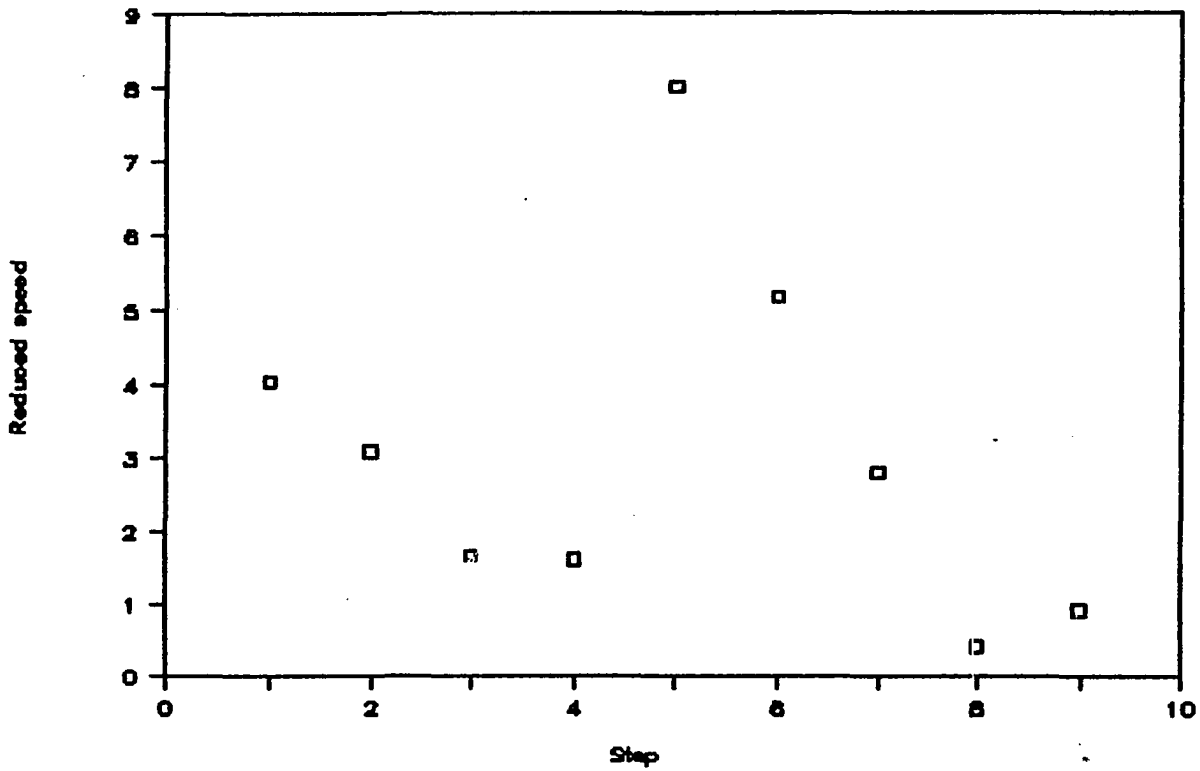


Figure 101. Reduced speeds for the width of the valve in R.bergonii in DSDP site 504.

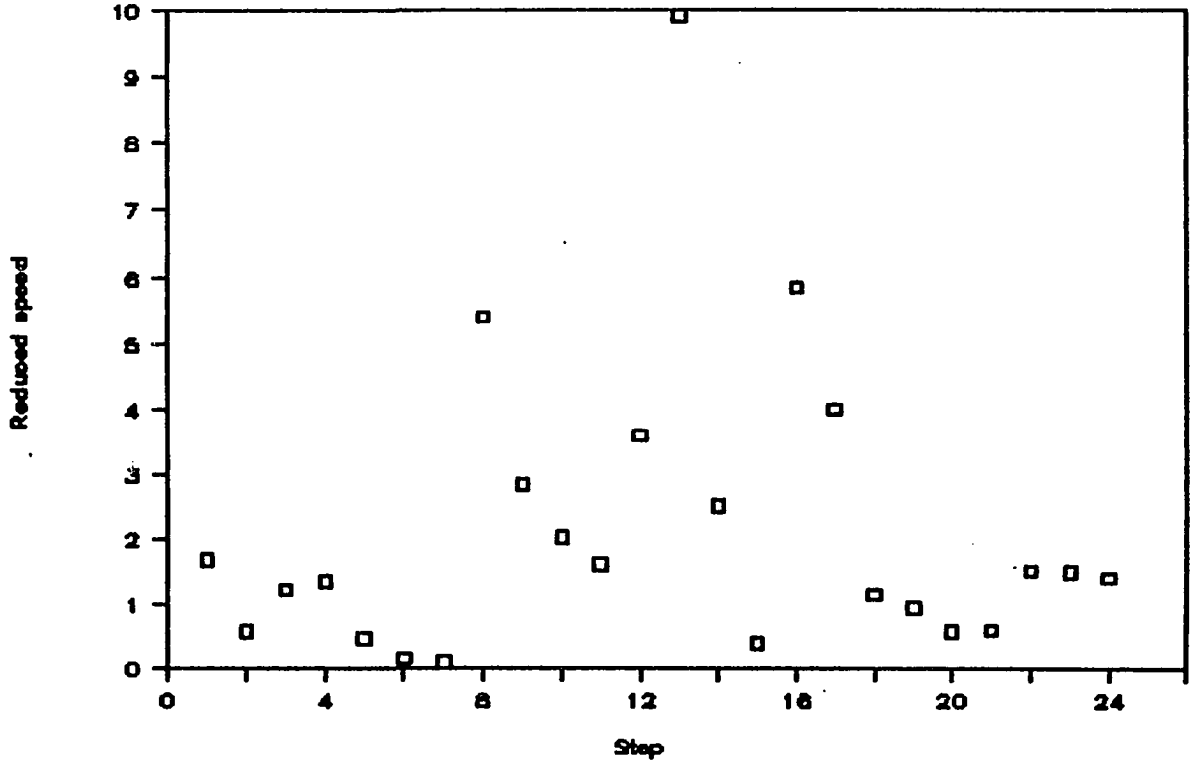


Figure 102. Reduced speeds for the width of the valve in R.bergonii in DSDP site 573.

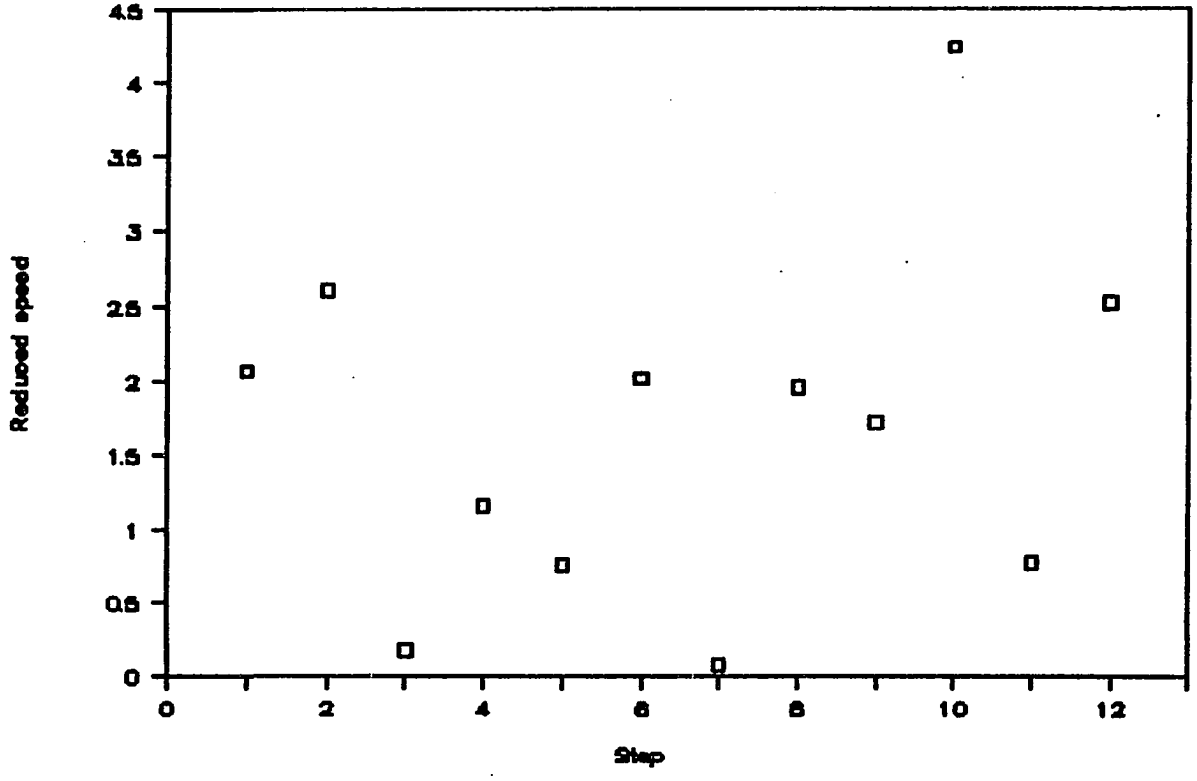


Figure 103. Reduced speeds for the width of the valve in R.bergonii in the Indian Ocean sites.

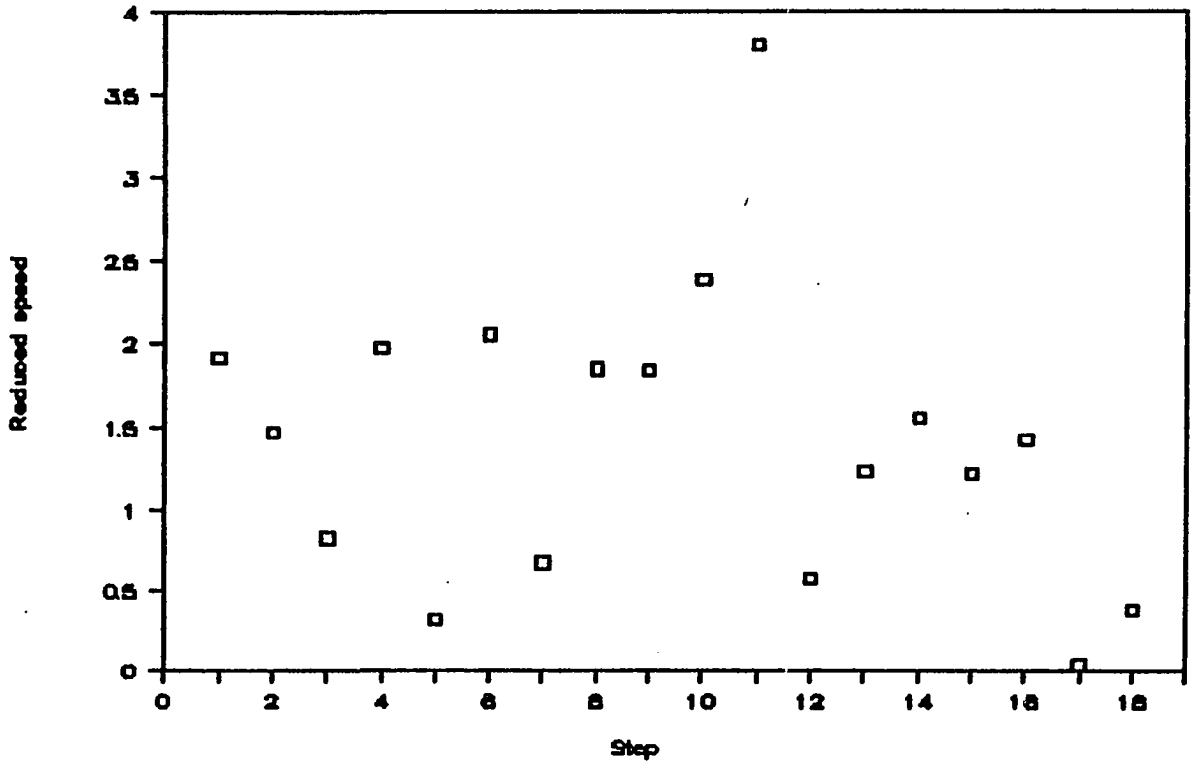


Figure 104. Reduced speeds for the width of the valve in R.bergonii in site RC12-66.

Appendix C.

The statistical procedures for fitting the hierarchical linear models presented in figures 39-41 on are described below. All the models in this study were fitted through linear regression techniques using the REG procedure in SAS (SAS User's Guide: Statistics, version 5, 1985). Each dependent variable (AL,HH and WC) was regressed upon time (T) or/and time levels shifted (S) (except for the model describing pure stasis or model 5) as well as on other "dummy variables" (also see Bookstein et al 1978, appendix I). The intercept is automatically included in all the regressions. The procedures are as following:

Model	Regress AL,HH or WC on	Definition of variable(s) (fig.39-41)
1	T	T=time level of sampling points for a lineage
2	S	S=time levels shifted (T_1-T_1 ; T_1-T_2. . T_1-T_n) for stage 1 and for stage 2 S=value of stage 1 at "bend"

Model	Regress AL,HH or WC on	Definition of variable(s) (fig.39-41)
3	S	Stage 1 S=value of stage 2 at "bend";stage 2 S=time levels shifted as described above
4	T,S	Stage 1 T=time level S=0; Stage 2 T=time level S= time levels shifted
5	P	Lineage 1 P=0;Lineage 2 P=1;P=Punctuation
6	S	Lineage 1 S=time levels shifted;Lineage 2 S=0
7	S	Lineage 1 S=time levels shifted;lineage 2 S=value of lineage 1 at furcation
8	T,S	Lineage 1 T=time levels S=0;lineage 2 T=time level S=time level shifted

Model	Regress AL,HH or WC on	Definition of variable(s) (fig.39-41)
9	S,P	Lineage 1 S=0,P=0;lineage 2 S=time levels shifted, P=1
10	S,P	Lineage 1 S=time levels shifted,P=0;lineage 2 S=value of lineage 1 at furcation, P=1
11	T,S,P	Lineage 1 T=time levels, S=0,P=0;Lineage 2 T=time levels,S=time levels shifted, P=1
12	S	Lineage 1 S=0;lineage 2 stage B S=time levels shifted, stage B S=value of stage B at the "bend"
13	S,P	Lineage 1 S=0 P=0;lineage 2 P=0,stage B S=time levels shifted, stage B S=value of stage B at the "bend"

Model	Regress AL,HH or WC on	Definition of variable(s) (fig.39-41)
14	S_1 , S_2	Lineage 1 S_1 =time levels shifted, S_2 =0; Lineage 2 stage B S_1 = S_1 for lineage 1, S_2 =time levels shifted; lineage 2 stage A S_1 = S_1 of lineage 1 at "bend", S2=value of stage B at bend
15	S_1 , S_2	Lineage 1 S_1 =0, S_2 =0; Lineage 2 stage B S_1 =time levels shifted, S_2 =0; Stage A S_1 =value of stage B at "bend", S_2 =time levels shifted
16	S_1 , S_2 , P	Lineage 1 S_1 =0, S_2 =0, P=0; Lineage 2 stage B S_1 =time levels shifted, S_2 =0, P=1; stage A S_1 =value of stage B at "bend", S_2 =time levels shifted, P=1

Model	Regress AL,HH or WC on	Definition of variable(s) (fig.39-41)
17	S_1, S_2, P	Lineage 1 S_1=time levels shifted, S_2=0, P=0; Lineage 2 stage B S_1=S_1 for lineage 1, S_2=time levels shifted, P=1; Stage A S_1=S_1=S_1 of lineage 1 at "bend" S_2=value of stage B at "bend", P=1
18	T, S_1, S_2	Lineage 1 T=time levels, S_1=0, S_2=0; Lineage 2 stage B T=time levels, S_1=time levels shifted, S_2=0; stage A T=time levels, S_1=value of stage B at "bend", S_2=time level shifted
19	T, S_1, S_2, P	Lineage 1 T=time levels, S_1=0, S_2=0, P=0; Lineage 2 stage B T=time levels, S_1=time levels shifted, S_2=0, P=1; stage A T=time levels, S_1=value of stage B at "bend", S_2=time level

shifted P=1

XVI. BIBLIOGRAPHY

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