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Growth Changes in the *Globorotalia fohsi* Lineage

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ABSTRACT

Chamber growth studies on the subspecies of the *Globorotalia fohsi* lineage indicate that important ontogenetic changes occurred in the phylogeny of this species. The origin and evolutionary levels within the lineage can be traced in the various growth changes that took place. Growth of chambers is not uniform but broken into two phases of geometric growth. The change from the first phase of growth to the second phase is abrupt and usually occurs between consecutive chambers. Significant increases in test size are effected by large increases in chamber size at the beginning of the phase two growth and also by large chamber sizes at the beginning of the phase one growth. The rapid changes in test size are tentatively explained by strong selective pressures brought about by a warming trend during Middle Miocene time. The sudden changes of growth phases seen in the *fohsi* lineage are viewed as a genetic mechanism by which new forms can arise rather suddenly. It is offered as an explanation for the abrupt appearances of some forms in the geologic record.

Introduction

The study of evolutionary change in planktonic foraminifera has usually focused on describing morphologic changes in shape and shell structure modification of the evolving lineage. In a few instances some biometric data has been included to emphasize the shape changes taking place. The parameters measured most often are the width, height, and breadth of the test. In this study attention has been directed at analyzing the changes in ontogenetic growth that take place during evolutionary change. Since evolutionary change involves growth changes manifested in morphologic changes, it would seem that a clear understanding of the fundamental changes in ontogenetic growth taking place in an evolving lineage should give a clearer insight into evolutionary change and, perhaps, into the taxonomic significance of such changes.

The coiled form of many organisms in nature was shown by THOMPSON (1966) to closely approximate a logarithmic curve. In the coiled test of a planktonic foraminiferan a tracing of the logarithmic curve is generated by the spiral suture. The logarithmic curve actually is a result of the geometric expansion of the chambers during growth (OLSSON 1971). The growth dimensions of the chambers are thus of far more importance in the analysis of evolutionary growth changes. OLSSON has also shown that there is an allometric growth relationship of chamber dimensions during growth of the individual that is fundamentally characteristic of the species. Even a single specimen contains much of the essential growth information of the species population, thus reflecting the genetic background of the species. Therefore, by measuring the growth dimensions of chambers during ontogeny one can gain an important insight into the genetic changes that are taking place during evolutionary change.

Method of Study

Figure 1 illustrates the basic construction model of a coiled planktonic foraminiferan. It shows the dimensions measured in order to determine the amount of growth

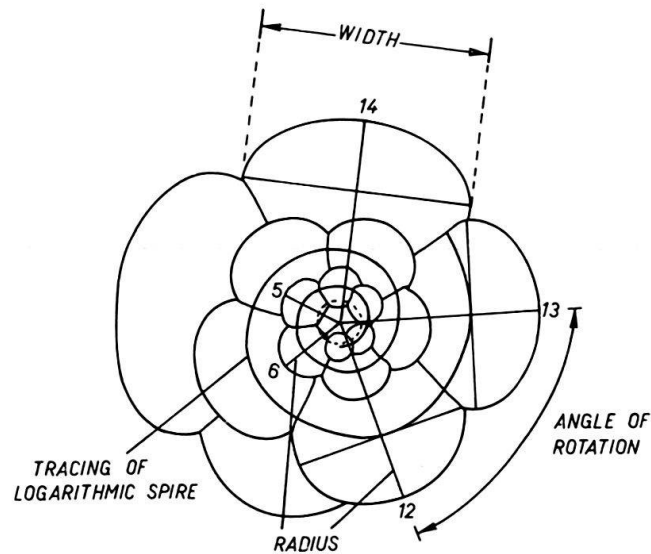


Fig. 1. Outline drawing of a coiled planktonic foraminiferan with little chamber overlap. Chamber width, radius (taken from center of proloculus to outer edge of chamber through the midpoint of the chamber), and angle of rotation (angle between midpoints of adjacent chambers) are the three growth measurements taken. The tracing of the logarithmic spire helps to illustrate the growth design evident in coiled planktonic foraminifera.

that takes place. These dimensions, the chamber width and the radius, are two of the three axes of a chamber that change their dimensions during growth of the individual and during evolutionary change. In this model ellipsoidal chambers are used since this shape is one of the common types observed in planktonic foraminifera. In the evolution of the *Globorotalia fohsi* lineage a change in chamber shape from ellipsoidal to conical takes place. As the geometric growth rate increases during this change chamber overlapping becomes significant so that only those parts of a newly secreted chamber (the anterior parts) from the point of overlap attachment are formed. Consequently the entire geometric form of the chamber is not generated. This is even true, of course, in loosely coiled forms with spherical chambers except that more of the geometric form of the chamber is visible. In taking measurements of chambers on those forms where there is much overlapping a rationale of reference points must be first analysed. In the *G. fohsi* series the chamber overlap amounts to approximately 50%. The chamber width measurement is taken from the midpoint to the anterior edge of the chamber and the value doubled (Fig. 2). This is important since the shapes of chambers are controlled by the chamber growth factors. The entire width dimension is needed as well in generating the growth curve of the individual and the species. Significant chamber overlap can be due to a lower angle of rotation between secretion of chambers or to an increased growth rate of chambers or both.

Measurements of chamber dimensions were made on scanning electron micrographs taken of specimens oriented to the spiral side (OLSSON, 1971). All measurements were adjusted to 100 times magnification for comparison of growth curves.

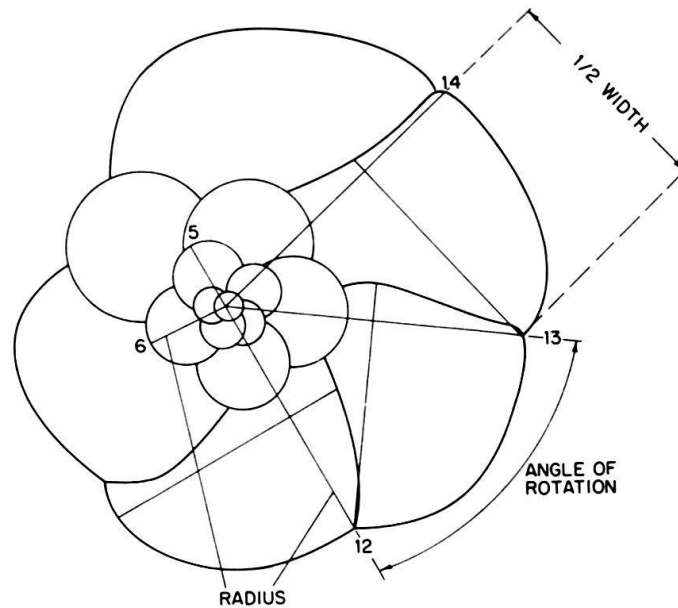


Fig. 2. Outline drawing of a coiled planktonic foraminiferan where overlap of chambers is approximately 50%. Only half the chamber width can be measured. Compare to Figure 1.

Specimens used in this study were taken from samples from the following localities:

Globorotalia mayeri

Globorotalia kugleri Zone, Cipero Formation, Trinidad, La Romaine, north of Mosquito Creek, Bolli ETH sample 407.

Globorotalia fohsi peripheroronda

Globorotalia dissimilis Zone, type locality, Cipero Formation, Trinidad, sample Bo 267 (see BOLLI 1957, p. 101); from *Globigerinita stainforthi* Zone, Cipero Formation, Cipero coast, Trinidad, sample K 9397; from *Globigerinatella insueta* Zone, type locality, Cipero Formation, Trinidad, sample Rz 108 (see BOLLI 1957, p. 101); from *Globorotalia fohsi peripheroronda* Zone, type locality, Cipero Formation, Hermitage pit, Trinidad, sample Bo 202 (see BOLLI 1957, p. 101, *Globorotalia fohsi barisanensis* Zone).

Globorotalia fohsi peripheroacuta, *Globorotalia fohsi praefohsi*

Globorotalia fohsi fohsi Zone, type locality, Cipero Formation, Trinidad, sample Bo 185A (see BOLLI 1957, p. 101).

Globorotalia fohsi fohsi, *Globorotalia fohsi lobata*

Globorotalia fohsi lobata Zone, type locality, Cipero Formation, Trinidad, Js 32 (see BOLLI 1957, p. 101).

Globorotalia fohsi robusta

Globorotalia fohsi robusta Zone, type locality, Cipero Formation, Trinidad, sample Bo 354 (see BOLLI 1957, p. 101).

Acknowledgments

The writer wishes to thank Dr. H.M. Bolli who kindly provided his samples of the *Globorotalia fohsi* lineage. Drs. Bolli and J.P. Beckmann reviewed various parts of the study. Scanning electron micrographs were taken by Mr. H.E. Franz of the Geological Institute of the Swiss Federal Institute of Technology. This work is partially supported by the Research Council of Rutgers University, New Brunswick, New Jersey.

The *Globorotalia fohsi* series

Figures 3–11 are growth curves representing the principal growth features of the *Globorotalia fohsi* lineage. Figure 3 illustrates the growth features of *Globorotalia mayeri* CUSHMAN and ELLISOR, the ancestral species of the lineage. Note the simple linear growth series of radius and chamber width indicating nearly perfect geometric growth. The growth limit of this individual can be observed in the slowing of growth of the last chamber. Since the radius and chamber width are growth related (that is, there is a corresponding growth increase of one dimension with another) they show an allometric relationship which is plotted in the lower part of the figure. Three types of allometric growth relationships can exist with respect to two dimensions. In the allometric equation of Figure 3 ($Y = -0.08 + 1.08 X$) the first part of the equation refers to the intercept on the Y axis when $X = 0$. The second part is the ratio of the geometric growth rates of radius and chamber width with respect to radius. When this ratio is equal to 1 or very close to 1 the dimensions can be said to be growing isometrically. When the ratio is less than 1 negative allometry can be said to exist (that is, the chamber width is increasing at a faster rate than the radius). Positive allometry exists when the ratio is greater than 1 (the radius increases at a greater rate than the chamber width). In this instance *G. mayeri* is growing nearly isometrically.

The growth features of *Globorotalia fohsi peripheroronda* BLOW and BANNER are shown in Figures 4–6. The origin of this subspecies would appear to be near the base of the *Globigerinita dissimilis* Zone. Figure 4 represents a specimen from that zone. The radius growth curve is straight illustrating nearly perfect geometric growth whereas the chamber width growth is broken into two phases of growth (here termed phase one and phase two). The allometric function is also broken into two phases. Phase one allometry is similar to that of *G. mayeri* in that growth is nearly isometric. However phase two exhibits negative allometry which indicates a greater rate of increase of the chamber width over that of the radius. This has led to significant overlapping of chambers in the phase two growth of approximately 50 per cent. The negative allometry of phase two growth seems to be characteristic of the subspecies in the lower parts of its stratigraphic range. Figure 6 shows the growth characteristics of the subspecies from the *G. fohsi peripheroronda* Zone. At this level in its range a second growth phase has developed in radius growth and the allometry of both phases is positive. Positive allometry of these phases seems to be a character of the subspecies in the higher parts of its stratigraphic range (Fig. 5 and 6). Phase two growth of radius and chamber width is established in two different ways. Phase two growth of chamber width begins after a large size increase has occurred whereas phase two growth of radius begins after a slowing down of growth. Positive allometry of phase two growth results (Fig. 6) because the geometric growth rate of the radius is greater than that of the chamber width. This has apparently led to some expansion of the coil.

Globorotalia fohsi peripheroacuta BLOW and BANNER is characterized by negative phase one allometry followed by high positive phase two allometry (Fig. 7). In phase two growth of radius and chamber width a pause in growth occurs at the juncture of phase one and two growth. This pause is followed by a slowing of the chamber width growth rate whereas there is an increase in the radius growth rate. This is the reason for the characteristic high positive allometry of the phase two growth in this subspecies.

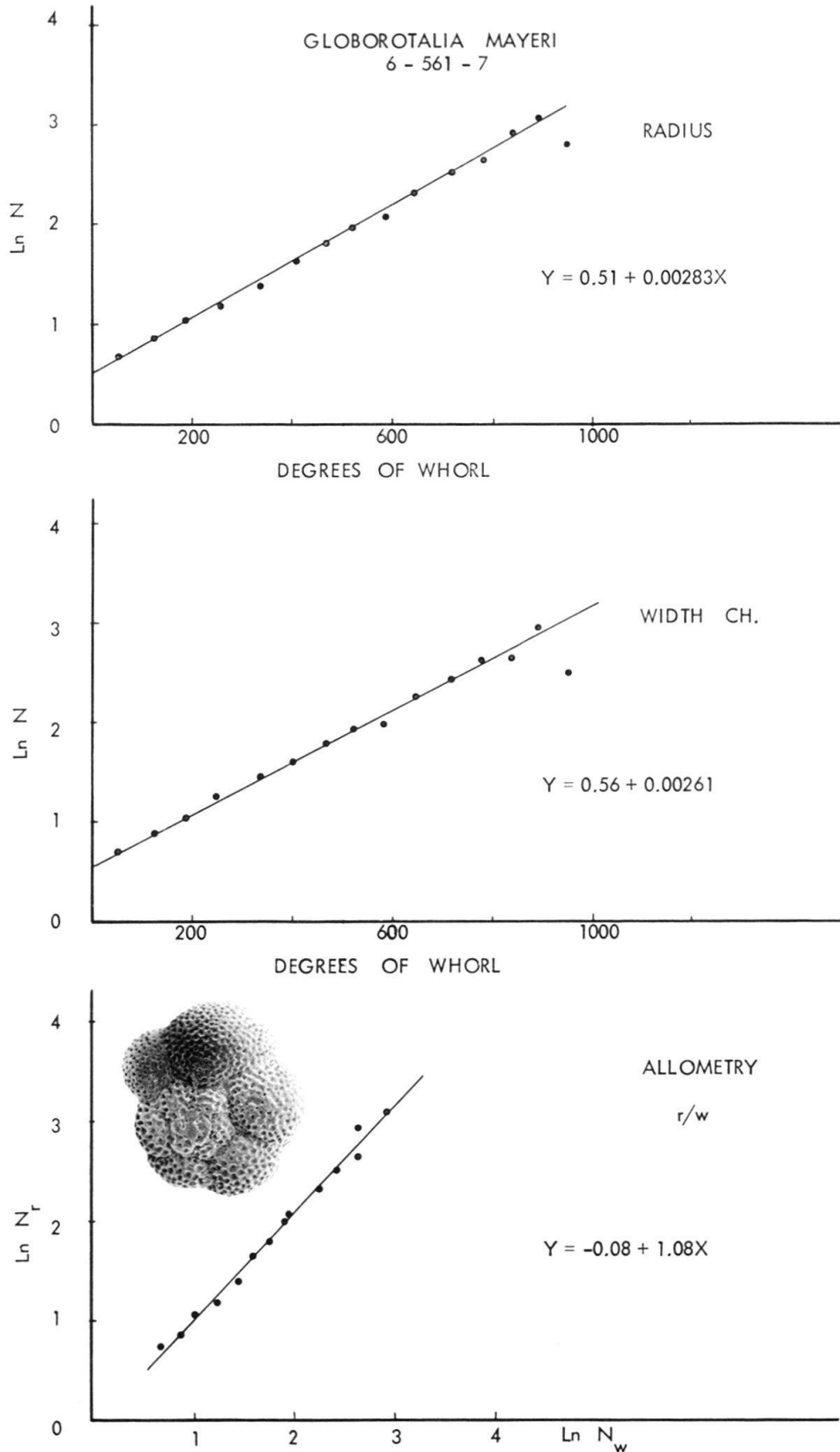


Fig. 3. Growth curves and allometry for radius and chamber width for one specimen of *Globorotalia mayeri* from the *Globorotalia kugleri* Zone. The number refers to the specimen reference number and scanning electron micrograph. The growth curve and allometric functions are understood to refer to the natural logarithms of the radius and chamber width. Each point represents a chamber. Chamber measurements are plotted according to accumulative degrees of whorl. Curves are fitted by Bartlett's "best fit" method. Final chambers that exhibit slowing of growth are not included in the allometric function. A natural log ($\ln N$) scale is used. Specimen $\times 75$.

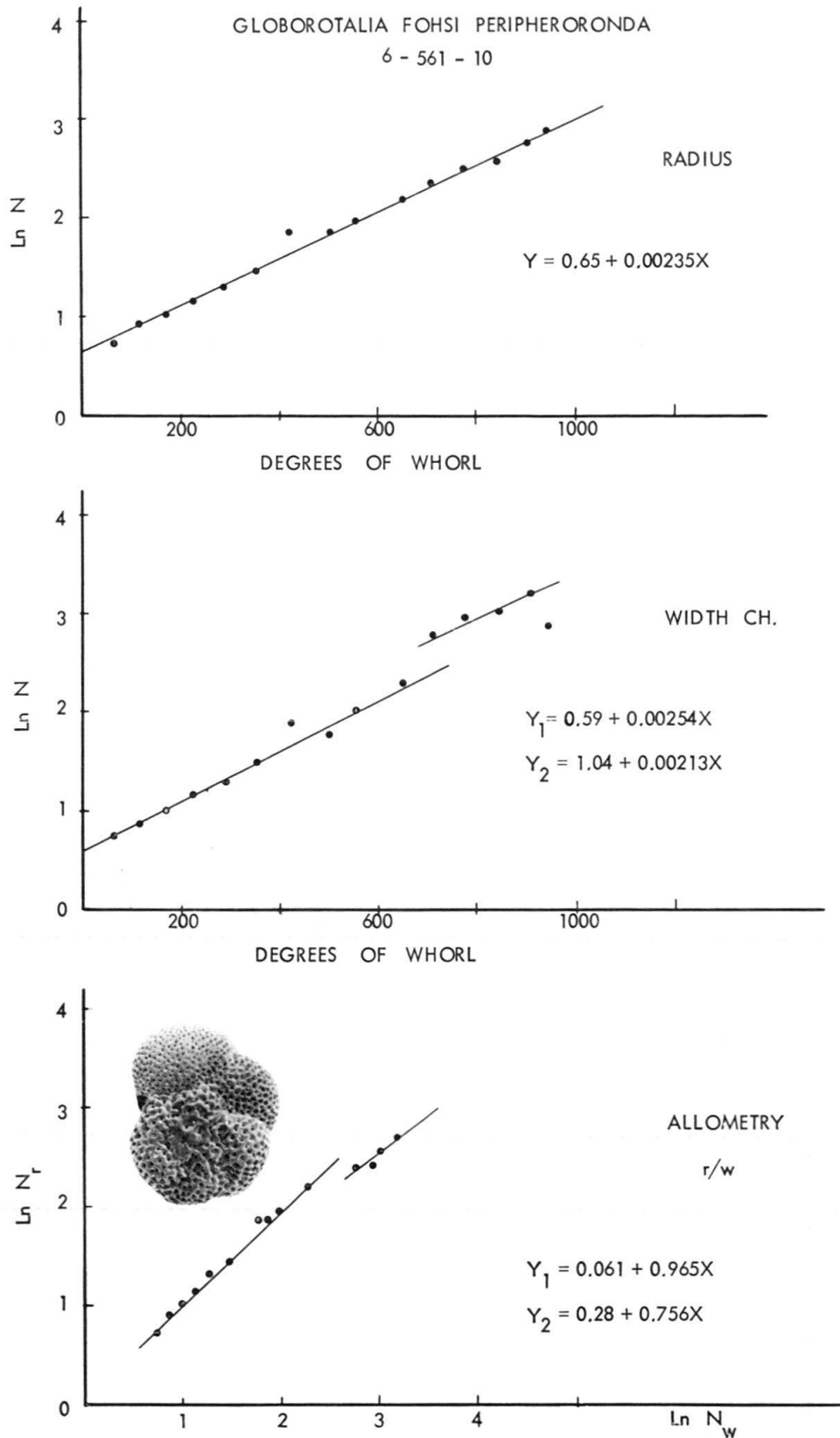


Fig. 4. Growth curves and allometry for radius and chamber width for one specimen of *Globorotalia fohsi peripheroronda* from the *Globigerinita dissimilis* Zone. See Figure 3 for explanation. Specimen $\times 75$.

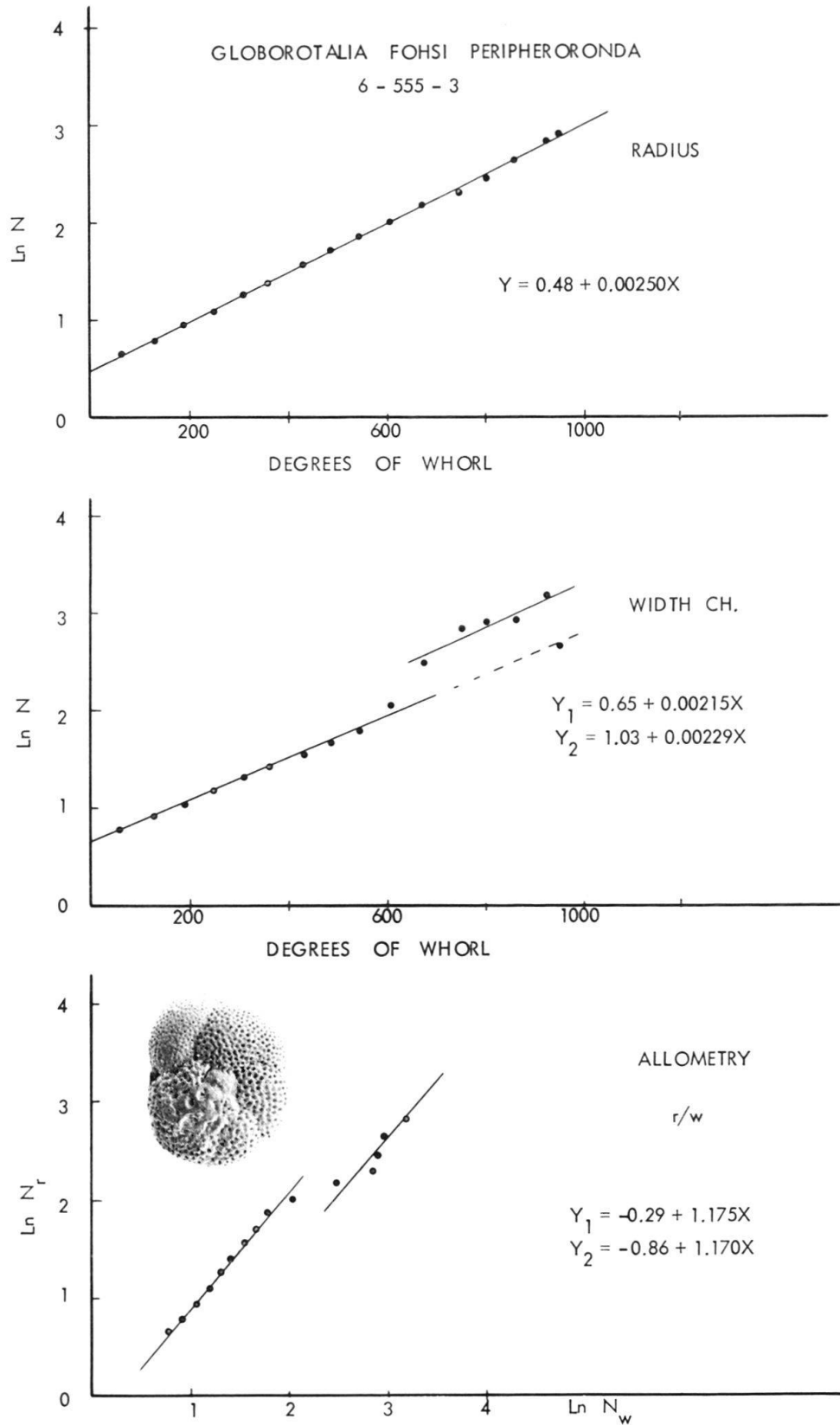


Fig. 5. Growth curves and allometry for radius and chamber width for one specimen of *Globorotalia fohsi peripheroronda* from the *Globigerinatella insueta* Zone. See Figure 3 for explanation. Specimen $\times 75$.

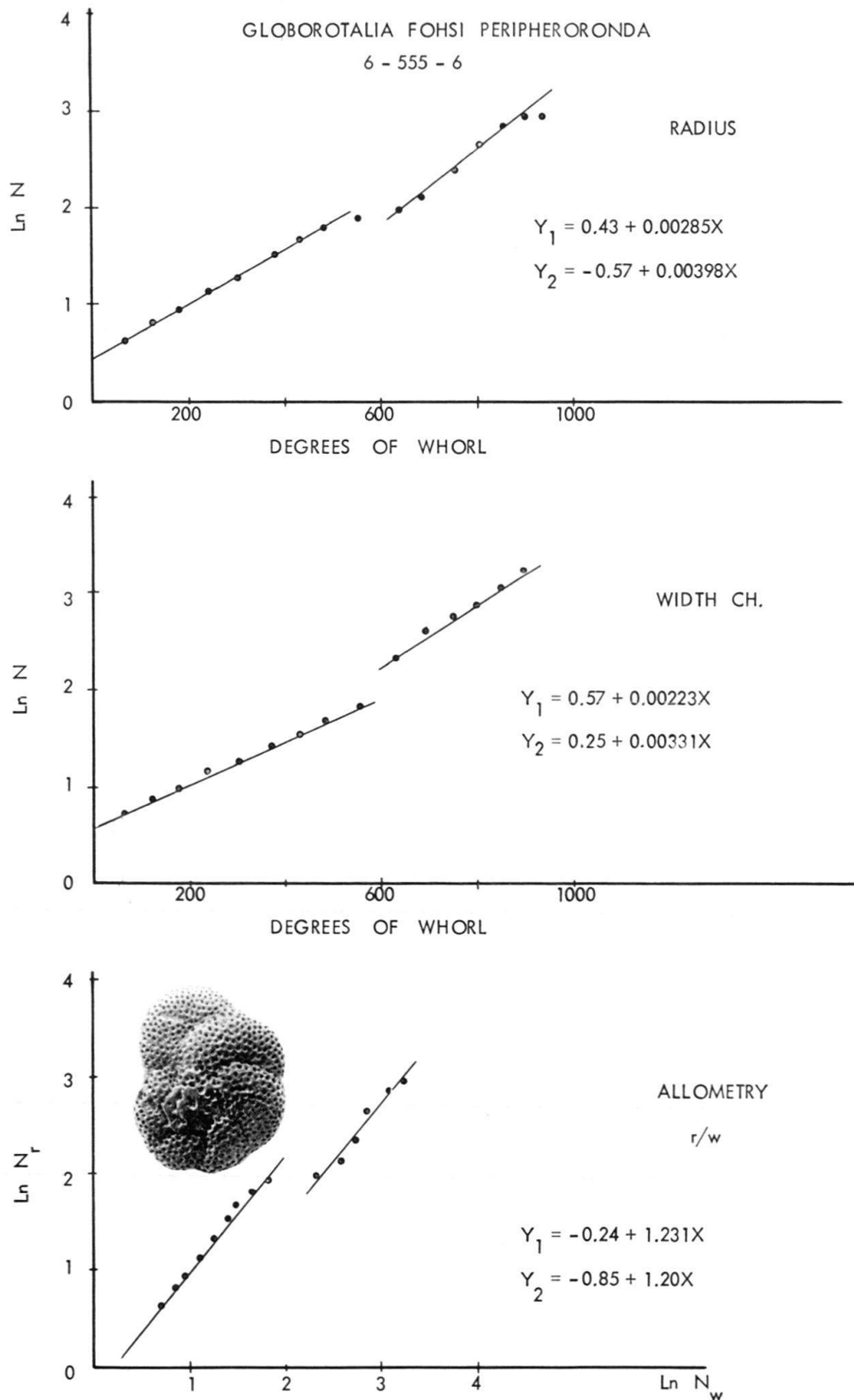


Fig. 6. Growth curves and allometry for radius and chamber width for one specimen of *Globorotalia fohsi peripheroronda* from the *Globorotalia fohsi peripheroronda* Zone. See Figure 3 for explanation. Specimen $\times 75$.

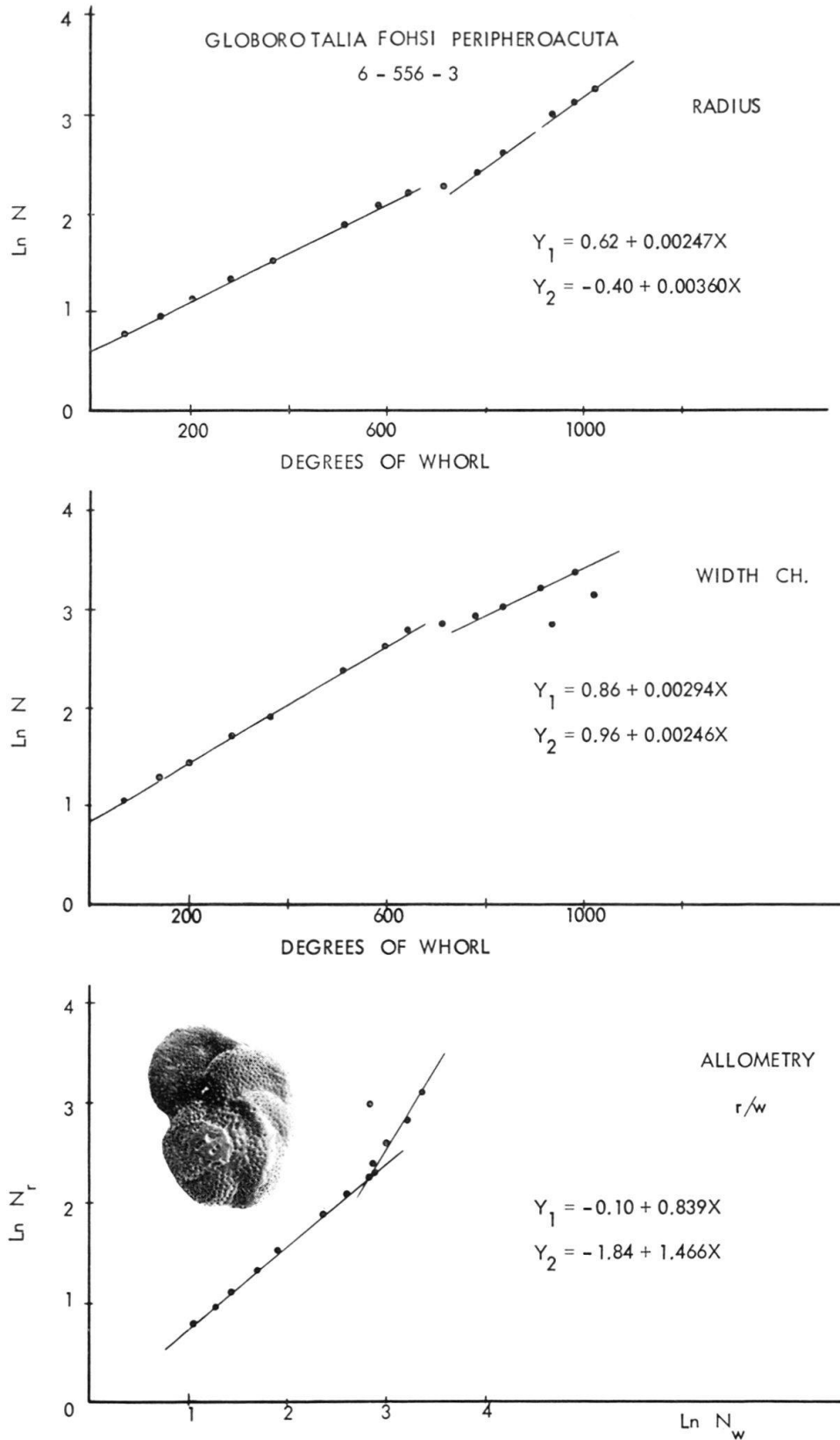


Fig. 7. Growth curves and allometry for radius and chamber width for one specimen of *Globorotalia foehsi peripheroacuta* from the *Globorotalia foehsi foehsi* Zone. See Figure 3 for explanation. Specimen $\times 56$.

The overall result has been towards a real increase in test size. When changes leading to size increase occur a balance of geometric proportions must be maintained otherwise rather unwieldy dimensions would result. In the case of *G. fohsi peripheroacuta* a third dimension (not measured in this study), that of the third chamber axis, has changed significantly. Conical chambers appear for the first time in the lineage in this subspecies. This is undoubtedly expressed in the growth rates of the two measured dimensions.

The subspecies *Globorotalia fohsi praefohsi* BLOW and BANNER and *Globorotalia fohsi fohsi* CUSHMAN and ELLISOR are characterized by positive phase one growth allometry followed by negative allometric growth in *G. fohsi praefohsi* and negative to nearly isometric growth in *G. fohsi fohsi* (Fig. 8 and 9). It can be observed from the growth curves of radius and chamber width that there is a significant increase in the size of the first chamber of phase two over that of the last chamber of phase one growth. It is this sharp growth increase that establishes a trend for a large overall increase in test size. Thus the allometric trends of phase two can be viewed as adjustment in growth proportions related to the increase in size. The test size increase is not only brought about by the phase two growth but also by that of phase one which has a higher size value at the beginning of growth than does *G. fohsi peripheroacuta* (Fig. 7, 8 and 9).

Globorotalia fohsi lobata BERMUDEZ is characterized by a negative phase one growth allometry followed by a generally positive trend of the phase two growth allometry (Fig. 10). A pause in growth at the juncture of phase one and phase two growth is observed. Initial growth in phase one is large with the geometric growth rate of chamber width being such that at the end of phase one growth a large test size has already been achieved. The pause in growth at the juncture of phase one and phase two growth and a slower rate of chamber width growth than previously prevents the test from becoming overly large and unwieldy. Nevertheless, a very great increase of test size has occurred. The chamber width growth rate in phase two is also large, however, and has led to the cockscomb chamber outline characteristic of this subspecies. Accompanying the increase in test size is an increase in the total number of chambers as well as a slight increase in the total degrees of whorl generated in test construction.

In the subspecies *Globorotalia fohsi robusta* BOLLI growth behaves as a single phase with slightly positive allometry (Fig. 11). The growth pattern is extremely interesting, however, because it is unlike that of *G. mayeri* (Fig. 3). Growth of the radius and chamber width is punctuated by several interruptions of reduced or negative size values. Growth rates of the intervals are all similar if not largely identical. In this case the consequences of the proportions of a large test size are kept under control by periodic pauses or even reductions in growth during an overall high growth rate. If the growth rates were allowed to continue without interruptions increasing overlapping of chambers and finally envelopment of the entire test would result. The growth proportions would not be maintained and an oolitic-like test secretion would occur; an obviously disadvantageous situation for a planktonic organism.

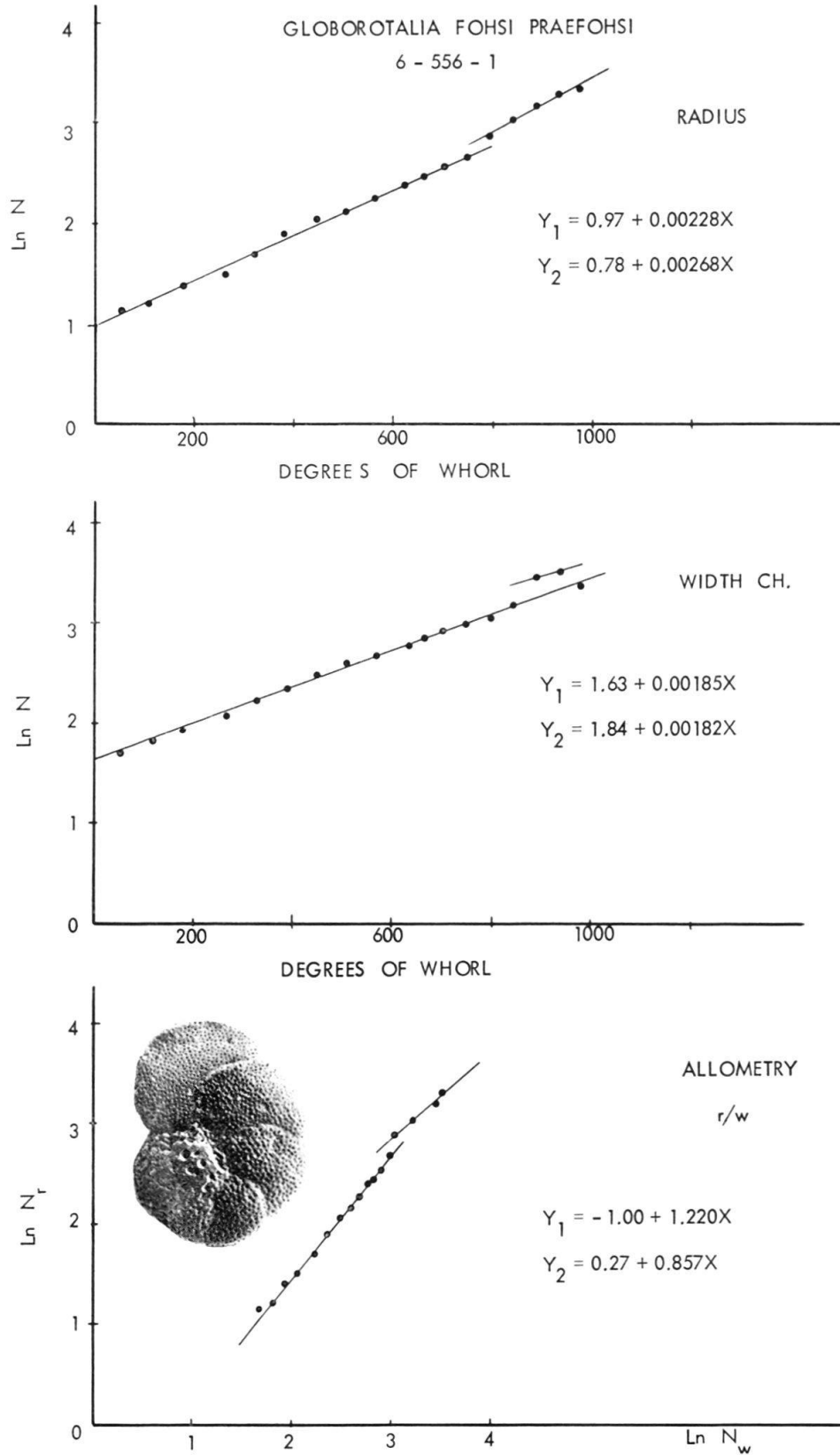


Fig. 8. Growth curves and allometry for radius and chamber width for one specimen of *Globorotalia fohsi praefohsi* from the *Globorotalia fohsi fohsi* Zone. See Figure 3 for explanation. Specimen $\times 56$.

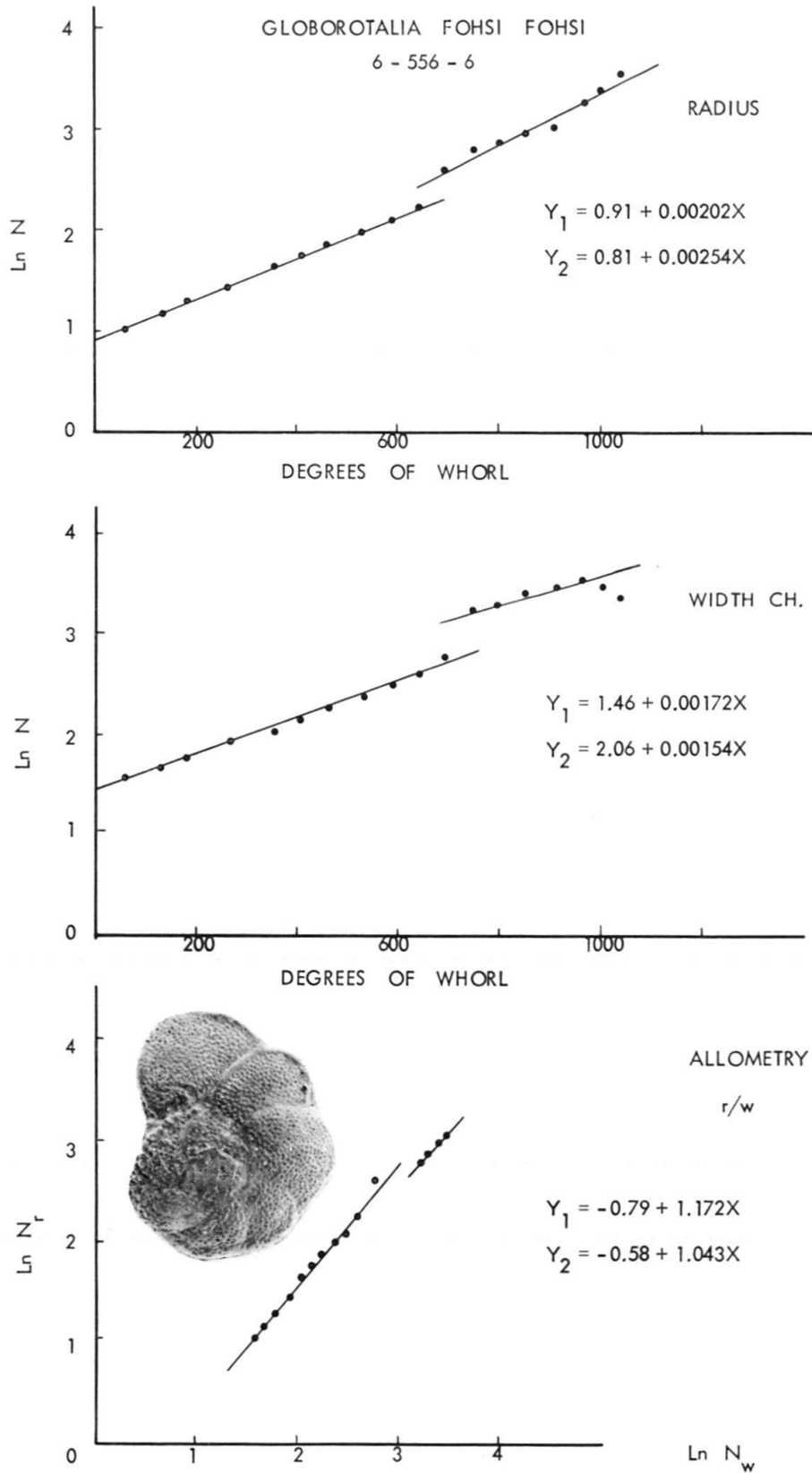


Fig. 9. Growth curves and allometry for radius and chamber width for one specimen of *Globorotalia fohsi fohsi* from the *Globorotalia fohsi lobata* Zone. See Figure 3 for explanation. Specimen $\times 56$.

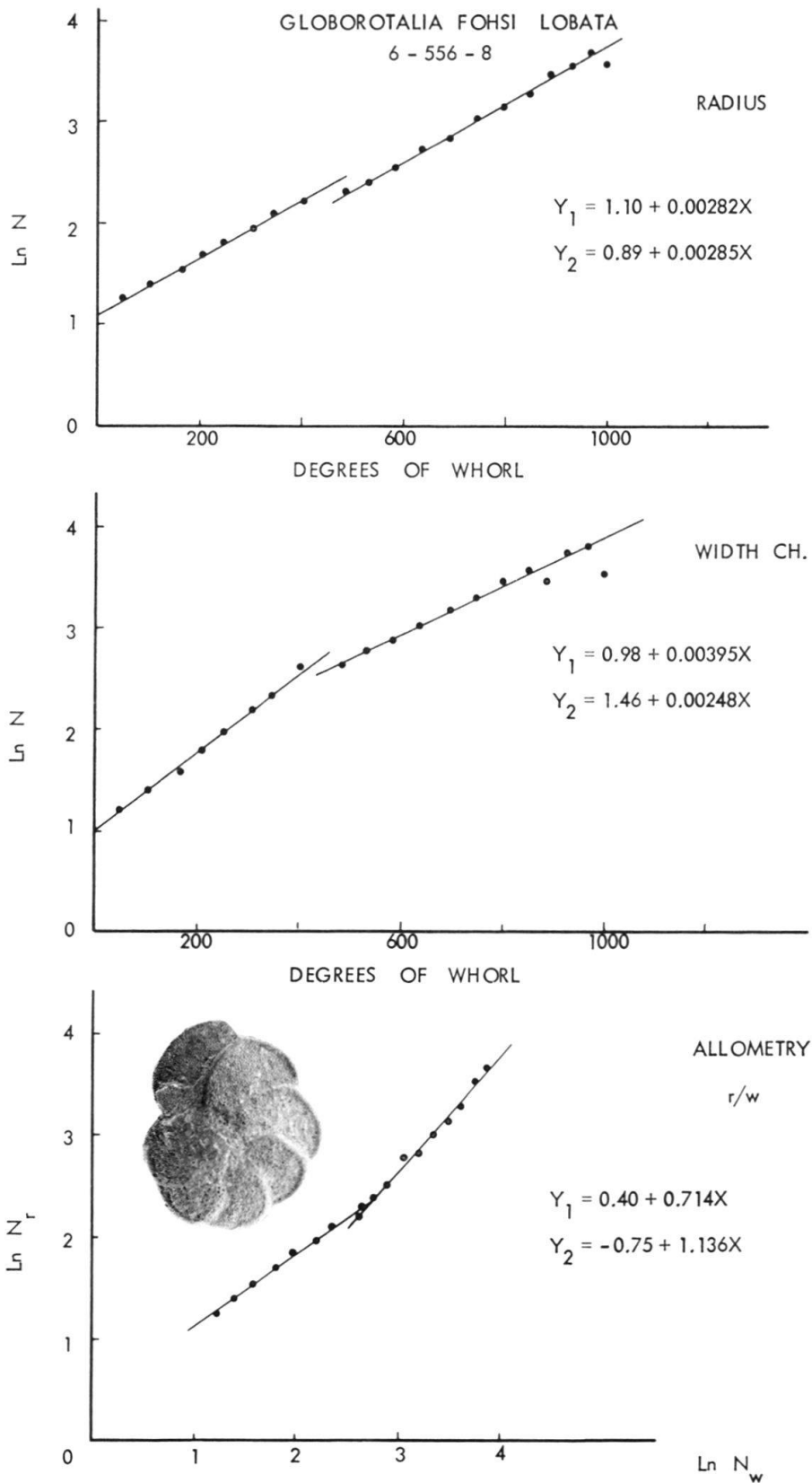


Fig. 10. Growth curves and allometry for radius and chamber width for one specimen of *Globorotalia fohsi lobata* from the *Globorotalia fohsi lobata* Zone. See Figure 3 for explanation. Specimen $\times 37$.

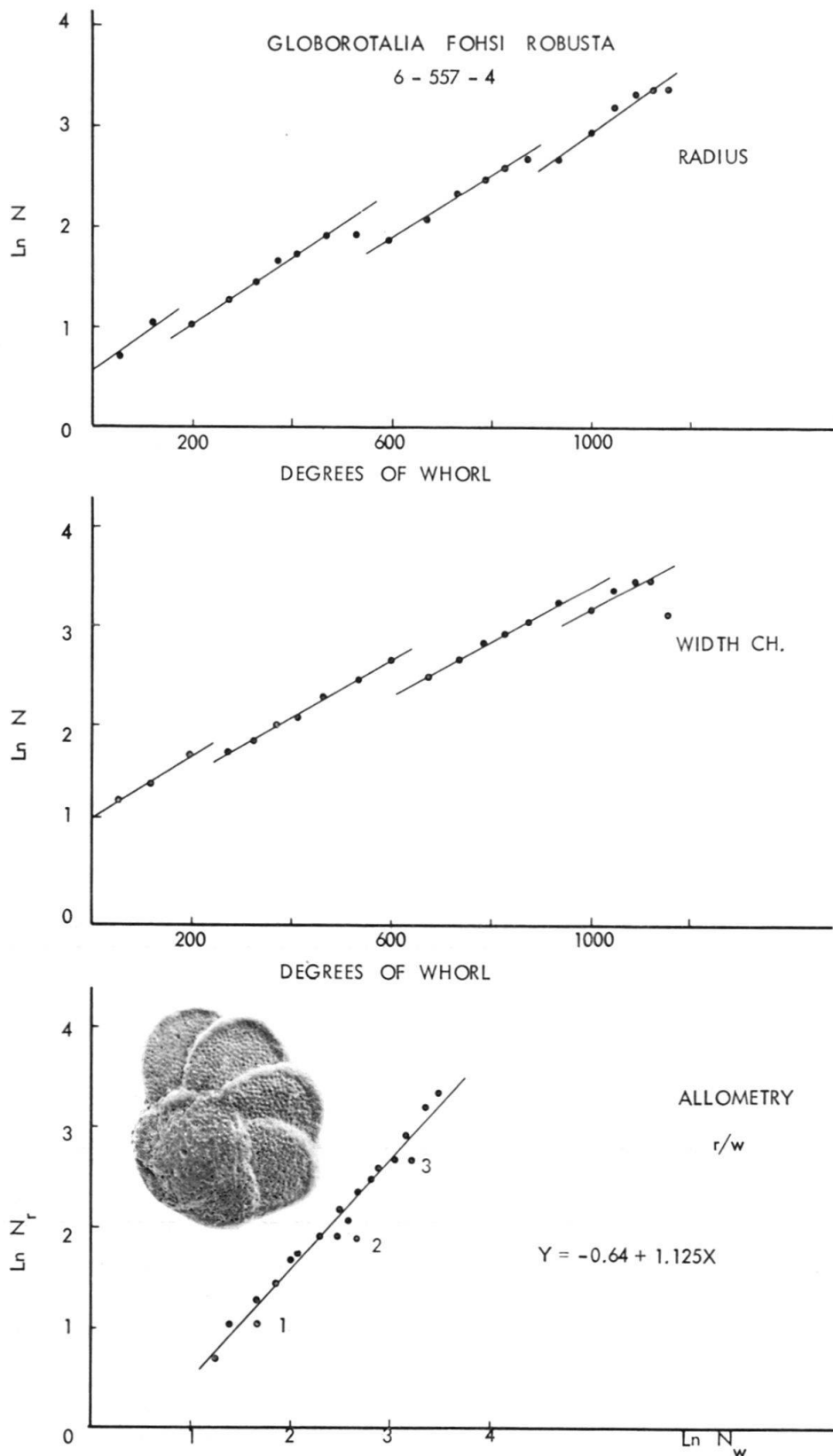


Fig. 11. Growth curves and allometry for radius and chamber width for one specimen of *Globorotalia fohsi robusta* from the *Globorotalia fohsi robusta* Zone. See Figure 3 for explanation. Specimen $\times 56$.

The allometric growth trend

The allometric growth trend of the *G. foehsi* series is shown in Figure 12. This is obtained by plotting A, the intercept of the allometric curve of each specimen on the

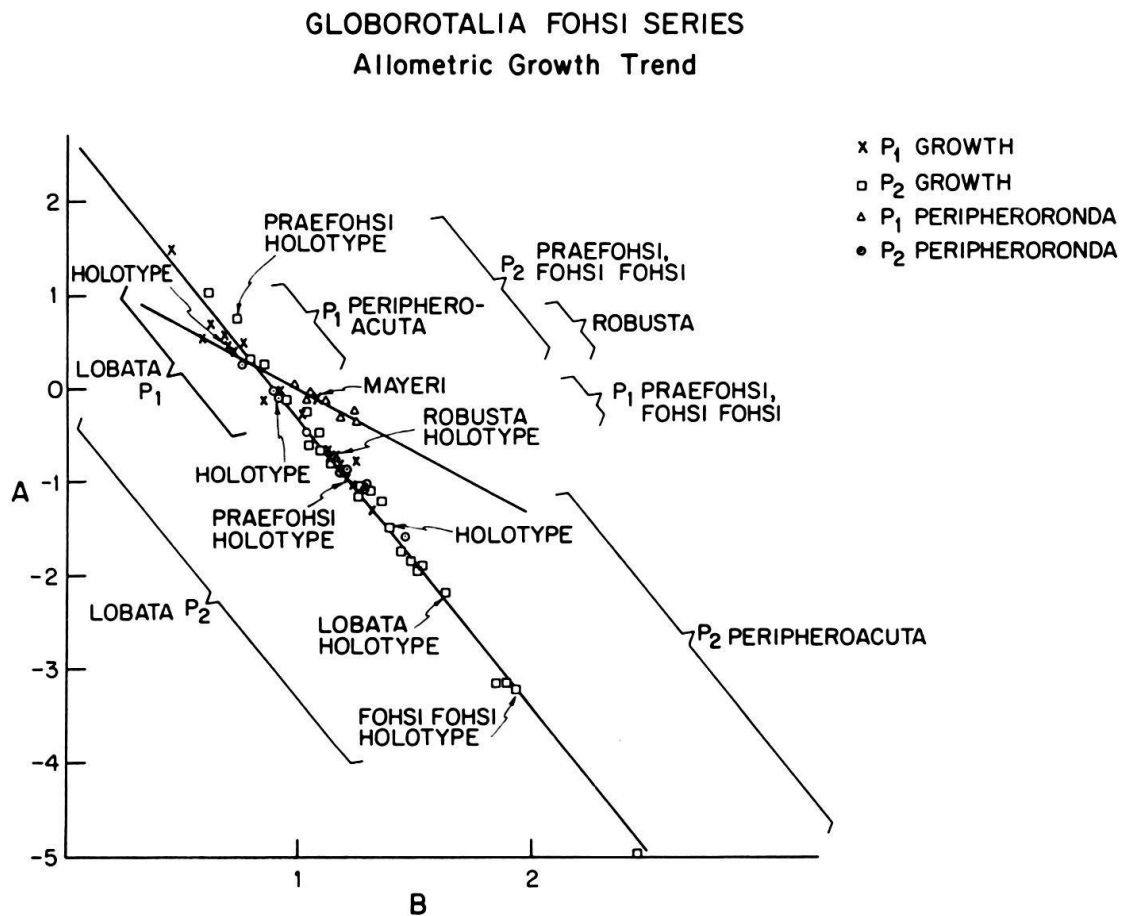


Fig. 12. Plot of the allometric functions of 33 specimens from the *Globorotalia foehsi* lineage. The two lines are fitted by Bartlett's "best fit". P₁ refers to phase one growth and P₂ refers to phase two growth.

Y axis, against B, the ratio of the geometric rates of increase of radius and chamber width for each specimen. The scatter of points defines a definite trend to which a "best fit" line can be drawn. The development of the *G. foehsi* series can be traced in the two allometric growth trends of figure 12. Note that *G. mayeri* growth and phase one growth of *G. foehsi peripheroronda* fall on the same growth trend, thus illustrating that the phase one growth characteristics of *G. foehsi peripheroronda* are the same as those of the ancestral *G. mayeri*. Note also that the grouping of points is very close. Preliminary data (OLSSON 1971) appear to indicate that species with but one growth phase tend to be very consistent in their growth patterns. This would seem to be the case with the above two taxa and demonstrates the close affinity of the ancestral and descendant species. Quite a different allometric growth trend is observed in the *G. foehsi* series. A very broad grouping of points is observed. Note, however, how the phase two growth of *G. foehsi peripheroronda* defines this new trend. The two growth phases of *G. foehsi peripheroronda* lie on different trends, the first on that of the ancestral species and the second on the new trend thus illustrating how the evolutionary

transition occurred. The establishment of the new trend appears to have occurred rather abruptly and possibly represents a quantum type of evolutionary change. All of the growth phases of the subsequent subspecies of the *fohsi* series fall on this new trend. In contrast to the more conservative cluster of points on the old trend a very broad growth field was established by the phase two growth of *G. fohsi peripheroronda*. The new trend is characterized by a wide spectrum of allometry, from strong negative to strong positive allometry. The overlapping of the various growth phases of the subspecies tends to support BOLLI's (1950, 1957, 1967) use of subspecies to illustrate the close genetic relationship between the taxa of the lineage.

A further extension of the geometric growth field was apparently established by *G. fohsi peripheroacuta* which developed from *G. fohsi peripheroronda* at the base of the *G. fohsi fohsi* Zone. It is at this point in the lineage that the first overall increase in test size occurs so that it is probably that the extension is the result of the size change. The largest size increase of the lineage occurred in *G. fohsi lobata* which also shows very similar growth characteristics to *G. fohsi peripheroacuta*. The similarity of growth characteristics (that is, negative phase one allometry and positive phase two allometry) between these two subspecies may be of real taxonomic significance or perhaps simply related to size growth. The subspecies *G. fohsi praefohsi* and *G. fohsi fohsi* also share similar growth features suggesting, here too, possible phylogenetic importance. Note that the phase one and two growths of these subspecies are at the opposite ends of the allometric growth trend from those of *peripheroacuta* and *lobata*. Morphologically there is much less difference between *praefohsi* and *fohsi* than between the latter two subspecies; the difference being in the development of a peripheral keel. In order to judge the validity of maintaining these two subspecies, the appearance of the keel should be studied in relation to stage of growth since it may be possible that its appearance on one or more chambers is a matter of how far ontogenetic development has proceeded. *Globorotalia fohsi robusta* because it grew with a single growth phase occupies a narrow field of the growth trend similar to that of *G. mayeri* and phase one of *G. fohsi peripheroronda*. It differs however in exhibiting pulsating growth rather than uniform growth. Allometry of *G. fohsi robusta* is isometric to slightly positive. In this characteristic it bridges the phase one and two growth of *G. fohsi fohsi* and *G. fohsi praefohsi*, perhaps suggesting that *robusta* may be more closely related to these subspecies than to, say, *G. fohsi lobata*.

In addition to the specimens used in this study the holotype figures of the subspecies of the lineage illustrated by BLOW and BANNER (1966) and BOLLI (1950) were also examined to determine how closely they fit the growth characteristics of the specimens used in this analysis. It is realized that the figures are line drawings and that it is not possible in all cases to gain reliable data on the early stages of growth. Nevertheless, it was considered important to have some data on the holotypes to match with that of the study. Only the phase two growth of the holotype of *G. fohsi peripheroronda* could be measured but it is observed (Fig. 12) that this plots on the new allometric growth trend of the series. The phase two growth of the holotype of *G. fohsi peripheroacuta* also falls within the growth field shown by the other specimens of this subspecies. The phase one and two growth of the holotype of *G. fohsi praefohsi* correspond as well to that observed in other specimens of the subspecies. The holotypes of *G. fohsi lobata* and *G. fohsi robusta* also exhibit the expected growth characteristics

anticipated by this study. The holotype of *G. fohsi fohsi*, which has been the subject of considerable debate, shows very strong positive allometry of the phase two growth. This places the holotype well outside the growth field exhibited in other specimens of this subspecies. It would appear that its growth characteristics are closer to those of *G. fohsi lobata*. Apparently the taxonomic concept of *G. fohsi fohsi* as expressed by various authors is not expressed in the holotype. The solution to this problem is, however, beyond the scope of this paper.

The various growth features exhibited by the lineage suggest additional research into the possibility that there is a more direct linkage of *G. fohsi peripheroacuta* to *G. fohsi lobata* than through *G. fohsi praefohsi*, and, also, that there is a more direct linkage of *G. fohsi praefohsi* through *G. fohsi fohsi* s.l. to *G. fohsi robusta*.

Size increase in the fohsi series

Perhaps one of the more significant characteristics of the *G. fohsi* lineage is the increase in size of the test observed in the various subspecies (BOLLI 1950, 1967 and BLOW and BANNER 1966). A slow increase in size was noted by them in the early part of the lineage which was followed by a large increase in size at the onset of the *G. fohsi lobata* Zone. They also observed that size leveled off and perhaps became regressive in the *G. fohsi robusta* Zone. Since the increase in the size of the test is due to the establishment of high growth rates of chamber dimensions the increase in size of the lineage has been restudied in relation to the changing growth dimensions of the chambers.

A useful measure of the rate of size change is the darwin, a unit devised by HALDANE (1949). It is given by:

$$d = \frac{\ln x_2 - \ln x_1}{t}$$

where t = the unit of time, one million years.

The difficulty of determining rates of size change in a fossil lineage is in estimating the amount of time duration of a zone and, in fact, the amount of time involved in the transition from one zone into another. Some time estimates are available (BERGGREN 1971) so that rough estimates on rates of size change can be made. The rates of size change (darwins) in the *fohsi* lineage is determined by taking the greatest chamber width measure of each subspecies in each zone and comparing it to that of subsequent subspecies in the next highest stratigraphic level. The absolute time values given by BERGGREN (1971) would appear to indicate that each of the *fohsi* zones and subzones (from *G. fohsi peripheroronda* to *G. fohsi robusta*) has a duration of approximately one-half million years. Because the subspecies of the lineage originate at the boundaries of zones size changes most likely occurred during the transition from one zone to the other. A shorter interval of time than that of the zone duration must be used to estimate rates of size change; this being the time duration of the transition from one zone into another. A reasonable estimate of time involved in the transition interval of zones would be in the order of a 100,000 years or less. Climatically induced faunal changes (zonal changes) probably occur over an interval of 10,000 years or less. In figure 13 the rates of size change (darwins) are based on the 10,000 year estimate.

increase involved in its evolution. Alternately, if *G. fohsi robusta* is derived from *G. fohsi lobata* a size decrease occurred. In either case the rate of change is the same, a fast rate of change. Thus it is observed that significant size changes were involved in the evolution of the *fohsi* series beginning with *G. fohsi peripheroacuta*. There is a possible causal relationship that might help explain the selective pressures that acted upon this series during the Middle Miocene.

Paleoclimatic evidence of various types (ADDICOTT 1969; DEVEREUX 1967; JENKINS 1968; and MARGOLIS and KENNETT 1970) from both hemispheres indicates an overall general cooling trend throughout the Miocene which is interrupted by a warming trend in the Middle Miocene. The warming trend would appear to encompass the interval occupied by the *fohsi* zones. The paleoclimate curve is drawn in (Fig. 13) and compared to the *fohsi* lineage. If this match is correct it appears that the interval of warming in the Middle Miocene provided the selective pressures that operated causing the rapid rates of size change in the *fohsi* series. Furthermore it can be observed that the selective pressures were effective throughout the entire interval, during amelioration and deterioration of the climate. The most rapid size change, that of *G. fohsi lobata*, appears to correlate with the peak of the warming cycle. The development of keels in *Globorotalia* is also an event generally associated with warmer water masses. As the evolution of the *fohsi* subspecies can be viewed as response to a warming climate trend, so can the final extinction of the lineage be viewed as a negative response to cooling of the climate. All of the responses to the selective pressures of a changing climate were very rapid.

The rapidity of genetic response to selective pressures that operated on the lineage can best be understood in terms of changing growth phases. Apparently evolutionary change can occur quite fast in the planktonic foraminifera by a sudden jump from one growth phase to another. It is largely this that leads to the rapid increase in size although it is also observed that initial growth of phase one begins with a larger size chamber in those subspecies registering the largest size increases. It would appear that evolutionary change can be quite rapid (quantum evolution) as well as gradual in the planktonic foraminifera. When viewed in this light the rather sudden appearances of some fossil types in the geologic record may be true manifestations of growth changes of the nature of those observed in the *fohsi* lineage. The results of this study support those authors who have thought in terms of special genetic responses to explain the sudden appearances in the fossil record of certain taxa (e.g., SCHINDEWOLF 1936, 1950) rather than those thinking in terms of a discontinuous record containing only certain parts of the evolutionary record. Abrupt changes in phases of growth appear to be a genetic mechanism by which rapid morphologic modification is brought about in planktonic foraminifera.

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