

# Analysis of the Extinction of the Late Cretaceous Foraminifer *Afrolivina afra*

M. M. Dodson

Department of Mathematics, University of York, Heslington, York YO1 5DD, England

and R. A. Reymont

Paleontologiska institutionen, Uppsala Universitet, Box 558, S751 22, Uppsala, Sweden

Received 15 November 1979 and in revised form 10 February 1980

M. M. Dodson and R. A. Reymont. Analysis of the Extinction of the Late Cretaceous Foraminifer *Afrolivina afra*. *Cretaceous Research* (1980) 1, 143-164. *Afrolivina afra*, a Late Cretaceous bolivinid foraminifer, became extinct in the Early Paleocene. It was succeeded by the smaller, morphologically similar species *Afrolivina africana*. Morphological variation in *A. afra* was in part correlated with environmental factors showing a pattern of random fluctuations about long-term ecological trends. A gradual, persistent and unbroken environmental trend, related to a eustatic fall in sea-level, is significantly correlated with the morphological evolution of the species. The micro-biogeography of *A. afra* at the time it was approaching extinction is consistent with its having given rise to *A. africana* allopatrically in a manner which can be described by a fold-catastrophe adaptive model. This model predicts that *A. afra* should undergo quantum evolution to *A. africana* in a restricted area in a near-shore environment.

However, detailed study of borehole material reveals an apparent parabolic increase in the overall size of *A. afra* prior to extinction and it is argued that as a result, *A. africana* cannot be the direct descendant of *A. afra* without there having been some "discontinuity" in the environment or evolutionary process. This suggests that the sudden replacement of a species by a smaller, morphologically similar form may not be a straightforward succession. The apparent parabolic increase in size of *A. afra* can be modelled by the fold catastrophe of Thom theory if interpreted as representing the initial phase of a form of adaptive quantum evolution in which a gradual environmental change causes a fitness peak to be absorbed into the flank of a higher peak.

In terms of such a model, the absence of a larger descendant species suggests that *A. afra* could have been replaced by *A. africana* before the quantum threshold had been reached. A possible cause for this could be that the changes in the environment might have lowered the height of the fitness function in the vicinity of the peak for *A. afra* to below that of the peak for *A. africana*, or vice versa.

Department of Mathematics, University of York, Heslington, York, YO1 5DD, England.  
Paleontologiska institutionen, Uppsala Universitet, Box 558, S751 22, Uppsala, Sweden.

KEY WORDS: *Afrolivina*; Evolution; Fitness function; Foraminifera; Species extinction; Thom theory.

## 1. Introduction

Although foraminifers are often abundant in borehole samples from Upper Cretaceous and Tertiary sediments, surprisingly little quantitative analysis of their evolution has been undertaken. Those studies that have been published (e.g. Bettenstaedt, 1962) have not been concerned with the detailed analysis of small changes in the morphology of the fossil species over a relatively short interval of time but rather with the identification of substantial shifts in morphology over long

intervals. For instance, Bettenstaedt (1962) concluded that the lineages of some Cretaceous foraminiferal species which he studied exhibited unidirectional size trends.

The main aim of this paper is to use the material available of *A. afra* from Western Nigeria to present quantitative evidence that the phenotypic response of this species prior to its extinction is consistent with a parabolic trend and, consequently, can be modelled by the so-called fold catastrophe of Thom theory. The material used here is relatively good although, of course, the data are by no means as precise nor as complete as in the physical sciences and there is considerable margin for error. Nonetheless, it must be said that any regular pattern of morphological change in an organism approaching extinction is unexpected and we think it is remarkable that the data agree reasonably well with a prediction derived from Thom's theory of catastrophes for the phenotypic response of an organism approaching the limit of its stability range (Dodson, 1975; 1976).

## 2. A note on the occurrence of *Afrolivina afra*

*Afrolivina afra* appeared during the Campanian. Its rise appears to coincide with the first and geographically more extensive of the two cycles of epicontinental transgressions and regressions which took place in the north and west African realm at the close of the Cretaceous (Reyment & Mörner, 1977). The conditions which prevailed then seem to have suited *A. afra* which flourished in an area of the West African coast stretching from the Senegalese coastal basin to the Angolan coastal basin (Castelain, Faulkner, de Klasz, Meijer & Rérat, 1962). During the Campanian era, and throughout most of the Maastrichtian, the species was very abundant, often completely dominating the fossil assemblages in which it occurs; in many borehole samples, it is the only animal microfossil found. Towards the close of Maastrichtian time and the onset of the regressive phase of the marine cycle, there was a gradually decreasing eustatic sea-level; *A. afra* became progressively less common and there was a marked shrinking in the geographical distribution of the species. By the initiation of the next transgression, the species was restricted to the Nigerian (and Camerounian) and Gabonese coastal basins (Castelain *et al.*, 1962; Castelain, 1966). Castelain (1966) noted that there is a stratigraphical break between the Maastrichtian and Paleocene in several of the West African coastal basins. The transition in Nigeria is, however, continuous (Berggren, 1960).

During the Early Paleocene, a period when the second epicontinental transgression reached its height, *A. afra* suddenly disappeared and seems to have been replaced by the smaller but similar species *Afrolivina africana* (Graham, de Klasz & Rérat), which was restricted to a small area in the Nigerian coastal sedimentary basin, the Camerounian basin and the Gabonese basin. (Reyment, 1966; Graham, de Klasz & Rérat, 1965.) Its life-span was very short and it appears to have died out before the close of the Paleocene. In all three areas, *A. africana* is preceded by *A. afra*.

## 3. The material of *A. afra* and its analysis

The material of *A. afra* was obtained from borehole samples from the deep-test Gbekebo I, drilled in Ondo State, Nigeria by the Shell-B.P. Petroleum Development Company of Nigeria Limited. Comparative material for the Cretaceous-Tertiary transition was available from another Shell-B.P. deep-test drilled at Araromi. A borehole drilled by Mobil Nigeria Limited at Afowo, near the international boundary with Bénin, shows that *A. afra* occurs in great abundance in the

sedimentary sequence south of Akisinde, the locality from which the sample of *A. africana* was obtained. This material derives from a borehole drilled by the Geological Survey of Nigeria in Ogun State. Accounts of the sequences at the latter two localities are given by Fayose (1970), and Reyment (1966), respectively. The locations of the localities mentioned in the text are shown in Figure 1. The boreholes penetrated sequences with no obvious stratigraphical breaks.

The samples from the Gbekebo borehole were obtained by wireline coring at discrete intervals. The pieces of core used in the present study come from some location within known intervals of 3 ft, thence the depth ranges given in the graphs.

With the exception of the sample from 2886 ft, which contains 73 specimens, the sample sizes are relatively small, varying mostly from 20 to 30 specimens.

### 3.1. The measurements

Nine characters or variables were measured on the megalospheric tests of the foraminifers, these being selected on the basis of a preliminary morphometric analysis of growth patterns (cf. Campbell & Reyment, 1978). The nine variables are indicated in Figure 2; they are:

1. Length of the test.
2. Maximum width in the plane of biseriality of the test.
3. Maximum breadth of the final chamber
4. Maximum height of the final chamber.
5. Maximum height of the penultimate chamber.
6. Diameter of the megalospheric proloculus.

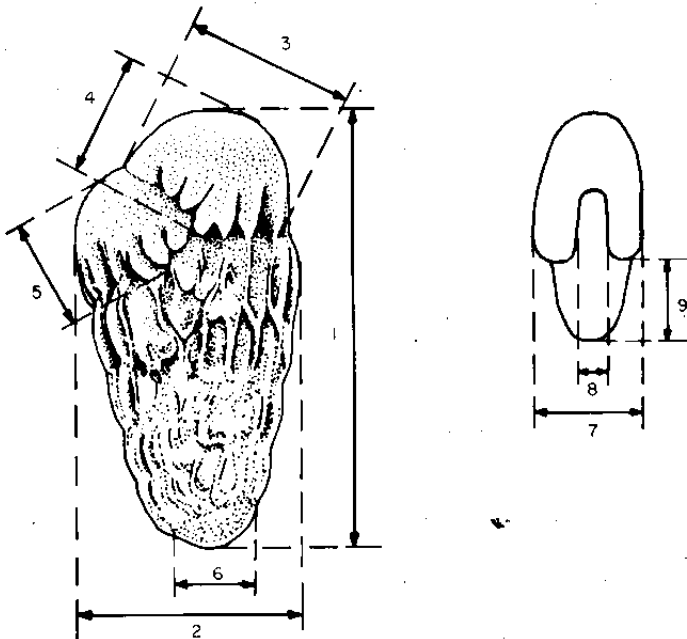


Figure 2. Sketch showing the characteristics measured on *Afrobolivina*. Length of test = variable 1, maximum width of test = variable 2, maximum width of last chamber = variable 3, maximum height of last chamber = variable 4, maximum height of second last chamber = variable 5, maximum diameter of the proloculus = variable 6, maximum breadth of test, measured at right

7. Maximum breadth of the test normal to the plane of biseriality.
8. Width of the aperture.
9. Overlap relationship between the last two chambers.

All specimens were measured on carefully calibrated SEM photographs. The SEM examination of microfossils has the added advantage that reworking can be identified with a greater degree of certainty than by routine optical examination. Reworked specimens were excluded from the study.

### 3.2. Life-cycle differences

The morphological differences caused by the alternation of generations in the life cycle of foraminifers are an important factor in their statistical analysis. The present material has been studied carefully in this connexion and it was found that 98% of the specimens are megalospheres. About the same condition was found for *A. africana* (Reyment, 1966). A significant source of unwanted variability in foraminiferal material derives from mixed samples of megalospheres and microspheres and from morphologic differences due to age-structuring in the samples. In all cases where age differences have been found to assume significant proportions, a growth-invariant transformation by Burnaby's method has been made (cf. Gower, 1976), or the equivalent shrunken canonical variate estimates of Campbell (cf. Campbell & Reyment, 1978) has been applied.

### 3.3. Statistical analyses

By inspecting the means of the uppermost six samples from levels 2901 ft to 2882 ft (corresponding to a time of roughly  $0.5 \times 10^6$  years), it can be seen that in the last three samples (levels above 2890 ft) seven variables show non-linear trend. Variable 8, the width of the aperture, shows a linear trend.

The four variables 3, 5, 7 and 9 increase over the last four levels (i.e. above 2892 ft) and variable 9 increases over the last five levels (i.e. above 2898 ft). The six measurements were plotted against borehole depth for a graphical appraisal of non-linearity. The results for variables 5, 7 and 9 are presented as examples of these plots; they are shown in Figures 3, 4 and 5. The vertical bars in these figures denote the 95% confidence intervals and the horizontal bars the depth range from which the samples were taken (cf. p. 146). It is evident that these variables do not increase substantially for the first 3 or 4 levels but augment steeply in the higher levels. It can be seen that a parabola can roughly be fitted to the highest five points for variable 9 (Figure 5). The fit for variable 5 is not so good, particularly in view of the relatively constant values at the lower levels.

The graphs 4 and 5 are obtained by estimating the co-ordinates ( $d^*$ ,  $p^*$ ) of the vertex of the parabola for each variable and then plotting  $\log(p^* - p)$  against  $(d - d^*)$ . The depth  $d^*$  is about 2880 ft for all of the variables and  $p^*$  is 34.5 for

Table 1. Means for six levels of *Afrolivina afra* in the Gbekebo borehole (in mm)

Depth of sample (feet)	N	Variables								
		1	2	3	4	5	6	7	8.	9
2901	22	1.222	0.535	0.437	0.309	0.296	0.175	0.430	0.044	0.143
2898	25	1.416	0.573	0.484	0.318	0.296	0.176	0.436	0.047	0.137
2892	41	1.469	0.543	0.440	0.305	0.297	0.175	0.424	0.044	0.140
2890	26	1.332	0.534	0.442	0.308	0.297	0.181	0.427	0.050	0.154
2886	73	1.585	0.618	0.514	0.347	0.318	0.163	0.486	0.050	0.157
2882	24	1.833	0.679	0.558	0.379	0.335	0.193	0.516	0.054	0.172

however, not great in relation to the size of the overall trend; they are, moreover, a common feature of borehole logs and are not always a result of primary sedimentary characteristics—a fracture acting as a water passage will produce a strong deflection. In the present case, however, the variants are not usually sharp “spikes” but tend to build up over a certain distance and fall off again equally slowly.

## 5. Thom's theory and the fold catastrophe

Classical mathematical analysis of natural phenomena by means of quantitative models aims at solving explicit differential equations exactly. The solutions will be analytic and so continuous. Consequently, with few exceptions, only relatively simple processes will be susceptible to a purely quantitative mathematical treatment.

For an important class of systems, however, there is a more qualitative approach developed by Thom (1975). Although usually applied to discontinuities in gradient systems, Thom's theory of catastrophes analyses the ways in which, in a general sense, the maxima and minima of potential functions can coalesce. When a potential minimum determining the state of a gradient system disappears, the system loses its stability until it assumes another stable state, corresponding to a new potential minimum. The change of state can be very sudden which is the reason for the choice of the term “catastrophe theory” for the subject.

In what is now known as Thom's theorem, it is shown that for “almost all” gradient systems where the potential has at most five parameters, discontinuous changes in the stable state caused by continuous changes in the parameters can arise in at most eleven essentially different ways, called “elementary catastrophes”. Our paper is concerned more with the geometrical aspects of the theory and how maxima and minima coalesce, rather than with discontinuities.

We note that the expression “almost all” used in the preceding paragraph means that the gradient systems or potentials for which the theorem does not hold form a small set and that to neglect them is analogous to neglecting the possibility of balancing a pencil on its point. Or, to use a comparison from simple probability theory, trials involving the toss of a coin ignore the possibility that the coin could conceivably land and remain balanced on its edge.

The potential functions for which the theorem holds are called “structurally stable” or “generic” and they are essentially unaltered by small perturbations or variations. It is worth emphasizing that unless there is a special reason for thinking otherwise, a potential function will in all likelihood be structurally stable or generic, so that it is reasonable to assume that a potential function of a natural process is structurally stable. We note that an explicit knowledge of the potential is not needed and that while the number of parameters in the potential function is limited to five, there is no restriction (except that it be finite) on the number of parameters required to describe the state. These reasons, and the similarity between stability and homeostasis, make Thom's theorem of interest for applications in biology.

The theory has been applied in physics, engineering, optics, and in some areas of biology. Fuller accounts of theory and applications are given in Thom (1975) and Zeeman (1977). The reduction in precision has not made the theory any less useful in the exact sciences.

As has been said, one aim of this paper is to present some quantitative evidence that prior to its extinction, the phenotypic response of *A. afra* can be interpreted as arising from the *fold catastrophe*, the simplest in Thom's classification and which we now explain. Naturally, it is not our intention to imply that no other model can be successfully applied to the observations.

Some of the concepts of Thom theory, and in particular the fold catastrophe, can

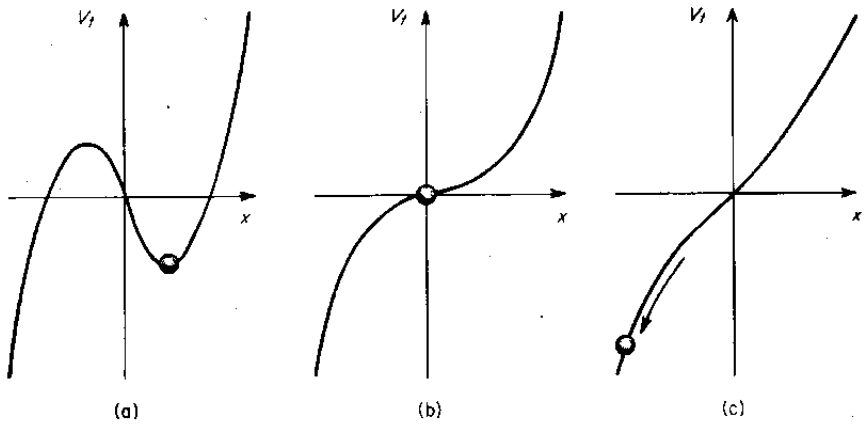


Figure 10. The bead on a wire. In 10(a),  $t < t^*$  and the bead is in stable equilibrium; its state  $x$  varies continuously with  $t$ . In 10(b),  $t = t^*$  and the minimum and maximum have annihilated each other; the bead is in neutral equilibrium at  $x = 0$ . In 10(c),  $t > t^*$  and the bead cannot remain stationary and so slides downwards.

be illustrated by a simple mechanical model. The potential function in this case has just one parameter and so, according to Thom's theorem, just one catastrophe, called the fold catastrophe, the simplest of the 11 elementary catastrophes, can occur.

Consider a bead threaded on a smooth, flexible wire, as shown in Figure 10. As the wire is pulled straight, gradually and continuously, the bead remains in stable equilibrium and its state or position varies gradually [Figure 10(a)] as the potential minimum where the bead is located is absorbed into the left-hand section of the wire. The intervening maximum grows smaller as the minimum is absorbed. We note that it is this period which is of interest to us in this paper. When the intervening maximum disappears [Figure 10(b)], the bead is in neutral equilibrium. Any further straightening, no matter how slight, of the wire results in the bead suddenly sliding irreversibly downwards [Figure 10(c)]. To analyze the onset of this "catastrophic" event more closely, we represent the wire by the graph of the function

$$V_t'(x) = x^3 + (t - t^*)x,$$

where  $t$  is a variable which determines the shape of the wire and may be taken as time. The case where  $t < t^*$  corresponds to the configuration in Figure 10(a),  $t = t^*$  to Figure 10(b) and  $t > t^*$  to Figure 10(c) (i.e. increasing  $t$  corresponds to straightening the wire).

Let the state of the bead be represented by its  $x$  co-ordinate. Evidently, the bead on the wire is a system, the state of which is determined by local minima (where the derivative  $V_t'$  vanishes) of a function  $V_t$  with a parameter  $t$ . As the parameter varies from values below the threshold at  $t^*$  to values above, a sudden, irreversible change of state occurs when the parameter exceeds the threshold  $t^*$ . The graph of the equilibrium state, given by the solution of the equation

$$V_t'(x) = 3x^2 + (t - t^*) = 0$$

is the parabola shown in Figure 11. When  $t < t^*$ , there are two equilibrium states, one stable and one unstable, corresponding to the wire having a maximum and a minimum at  $t$ . The upper half of the parabola is the locus of the stable equilibria and shows how the state or position of the bead varies with the parameter  $t$ . More

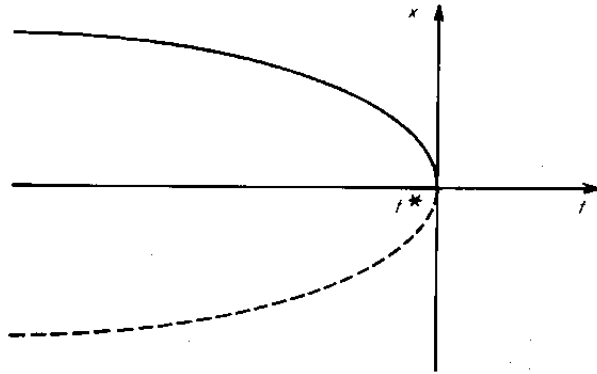


Figure 11. The graph of the solution of the equation  $3x^2 + (t - t^*) = 0$  giving the equilibrium states of the bead on a wire. When  $t < t^*$ , there are two equilibrium states, one stable corresponding to the bead being at a local minimum (continuous line), the other unstable, corresponding to the bead being at a local maximum (dotted line). At  $t = t^*$ , the minimum and maximum coalesce, giving rise to a threshold. There are no equilibrium states for  $t > t^*$ .

precisely, up to the threshold  $t^*$ , the stable equilibrium  $x$  is given by the equation

$$x = \{1/3(t^* - t)\}^{1/2}; \quad (1)$$

there are no equilibrium states for  $t > t^*$ .

Note that this does not mean the bead continues to slide down the wire for ever and there may well be another minimum beyond the length under consideration. Evidently, apart from its continuing to descend (which corresponds to the state continuing to decrease), little can be said about the descent of the bead before it reaches another minimum and it must be stressed that the above analysis applies in the vicinity of the disappearance of a minimum.

It is nonetheless remarkable that Thom's theorem asserts that this relatively simple behaviour is typical in the sense that just before its absorption into the side of the lower minimum, a minimum can be safely assumed to follow a parabolic path. Thus, on approaching the threshold at  $t^*$ , the minimum on which the bead rests is absorbed into the left hand section of the wire; the intervening maximum of the wire is reduced and the distance of the bead from the origin decreases parabolically to 0. (We recall that the expression "virtually any" means that ignoring the gradient systems for which the theorem does not hold can be likened to ignoring the possibility of balancing a pencil on its point.)

Many of the features of the above system will depend on the precise shape of the wire, the choice of coordinates, and so on. Except, however, for a set of shapes which can be safely ignored, sufficiently near the threshold, the exponent  $1/2$  in equation (1) does not depend on the wire being exactly a cubic. For more complex systems with a potential parametrized by  $t$ , but where the state is given by  $n$  parameters  $x_1, \dots, x_n$ , it can be safely assumed that just prior to a threshold  $t^*$

where the minimum disappears into the flank of a lower, neighbouring minimum, the equation

$$\sum_{i=1}^n a_i(x_t - x_i^*) = (t^* - t)^{1/2}, \quad (2)$$

where  $(x_1^*, \dots, x_n^*)$  is the value of the state at  $t^*$  and  $a_1, \dots, a_n$  are constants, holds. Moreover, the state  $(x_1, \dots, x_n)$  can be represented by a single, essential variable  $y$ , say, and for values of  $t$  just less than  $t^*$ ,

$$y - y^* = K(t^* - t)^{1/2}, \quad (3)$$

where  $y^*$  is the value of  $y$  at  $t^*$  and where  $K$  is some constant. As with the bead, there are no stable states near  $y^*$  when  $t$  is greater than  $t^*$ . Once the threshold has been crossed, little can be said about the subsequent change of state, except that the next stable state will be bigger or smaller according as the state  $y$  is increasing or decreasing respectively (i.e. according as  $K$  is negative or positive) prior to the threshold at  $t^*$ . Parameters which do not change suddenly are called inessential and near the threshold will either vary linearly or remain constant.

## 6. The environment, the phenotype and the fitness of *A. afra*

In order to discuss the application of Thom's theorem to the rapid increase in size of *A. afra* prior to its extinction, precise definitions of environment and phenotype are needed. Now, since *A. afra* was a marine organism, then providing the sea-level of its habitat were not too low, its (presumably interstitial) environment would have been homogeneous (i.e. no discontinuities) and uniform (i.e. the same for each individual in the population). The environment can be specified by a sufficiently long (but finite) list or  $m$ -tuple of real numbers  $(e_1, \dots, e_m)$ , where for example,  $e_1$  might be the depth of the sea,  $e_2$  the salinity,  $e_3$  the temperature, and so on. The uniformity of the environment of *A. afra* ensures that the environment is determined by the time or by the depth of the borehole (i.e. some particular borehole depth is located at some particular phase in the environmental history of the sedimentary pile). Thus, the environment is a function of time or of borehole depth  $d$  say.

Away from the immediate coast, the effects of the Late Cretaceous fluctuations in sealevel on the environment of *A. afra* would have been gradual and smooth (i.e. without sharp fluctuations). If the sedimentary material were also deposited regularly, then it would follow that the environment depends smoothly on the borehole depth  $d$ . In mathematical language,

$$e = g(d),$$

where  $e$  denotes  $(e_1, \dots, e_m)$  and where  $g$  is a (vector-valued) smooth function. In western Nigeria, the fossil record throughout the existence of *A. afra* is continuous and there are no stratigraphical breaks (Berggren, 1960). This, together with the gradual changes to which the environment of *A. afra* was subject (the Late Campanian to Early Maastrichtian transgression and the Late Maastrichtian regression—both of which are large-scale events in the history of the South Atlantic), makes it reasonable to suppose that the environment of *A. afra* can be expressed as a smooth function of the borehole depth  $d$ .

Of course, the marginal zone of the sea would not have been homogeneous nor uniform and the changes, such as the flooding or formation of lagoons, caused by rises or falls of sea-level, need not have been gradual nor smooth. The further significance of this observation is taken up later.



The phenotype of an individual can be specified by a sufficiently long (but finite) list or  $n$ -tuple of characters. The phenotype of a population whose members are of different ages, sexes or even, as has already been mentioned for *A. afra*, belong to different phases in the foraminiferal life cycle, presents problems. Nevertheless, a mean phenotype  $(p_1, \dots, p_n)$  say, can be defined by using suitable samples and by using a statistical transformation which brings about growth invariance (see, for example, Gower, 1976). For convenience, we shall denote  $(p_1, \dots, p_n)$  by  $p$ .

Darwin's law of natural selection implies that natural selection tends to increase the fitness  $f(e, p)$  (or decrease the misfitness  $-f(e, p)$ ) of a population in a given environment  $e$  by modifying the phenotype  $p$ . Since the palaeo-environment is assumed to be varying smoothly with borehole depth  $d$ , we can speak of the fitness  $f(d, p)$  of *A. afra* at a borehole depth  $d$ , instead of its fitness  $f(e, p)$  in an environment  $e$ . (Strictly speaking, we should use a different function, say  $F(d, p)$ , where  $f(d, p) = f(g(d), p)$ , but it is not necessary for our purposes.) It is clear that the borehole depth  $d$  is a parameter for the fitness  $f$  and should be compared with the parameter  $t$  introduced in the discussion in Section 5 with respect to the bead on the wire.

It is usual to assume that providing no thresholds are crossed inside their stability range, wild populations in a slowly varying environment remain maximally fit or, to use Simpson's terminology, remain at an adaptive peak (see, for example, Eldredge & Gould, 1972, p. 94). Thus we assume that *A. afra* was maximally fit while inside its stability range or until it disappeared.

Returning once more to the example of the bead on a wire, the threshold at  $t^*$ , where the minimum disappears, corresponds to the threshold depth  $d^*$  where the fitness peak for *A. afra* disappears, i.e.  $d^*$  represents the limit or edge of *A. afra*'s adaptive stability range. These ideas, which are discussed more fully in Dodson (1975; 1976), have some similarities with the familiar Simpson-Wright selection landscape, where the adaptive peaks in the landscape correspond to local maxima of the fitness. The point of view taken here, however, differs from that of the Simpson-Wright model in a number of respects. Firstly, the mean phenotype is considered, so that the population is represented as a point on the landscape instead of a region. Secondly, the landscape is not confined to being a two-dimensional surface but is a high-dimensional space which varies with time (or depth). Actually, little will be lost by thinking in terms of a two-dimensional selection landscape or fitness surface or, indeed, of a one-dimensional fitness curve, corresponding to the phenotype being represented by a single variable. Thus, in Figure 12, the variation with depth (or time) of the fitness curve corresponding to a single phenotypic variable of *A. afra* (e.g. variable 9) is shown as a surface in which the fitness peaks corresponding to *A. afra* form a ridge running into the right-hand ridge of higher peaks.

Thirdly, we have assumed that the mean phenotype maximizes the fitness locally, i.e. that the mean phenotype is located at an adaptive peak, except after the peak disappears. Hence, allowing for the opposite conventions governing fitness and potential energy, the mean phenotype can be compared with the bead on the wire, discussed above. The point representing the value of the phenotypic variable which maximizes the fitness locally can thus be envisaged as moving along the top of the left-hand ridge towards the higher right-hand ridge. The path traced out in the  $(d, p)$  plane beneath this surface by the shadow of this point at the fitness peak is simply the graph of the phenotypic variable against depth (or time).

Now, Thom's theory gives a mathematical description of the typical trajectory or path of a fitness or adaptive peak as it approaches the flank of a neighbouring peak. Indeed, under the additional assumption that the fitness is a smooth function of the phenotype  $p$  and the depth  $d$ , Thom's theorem asserts that it is virtually certain

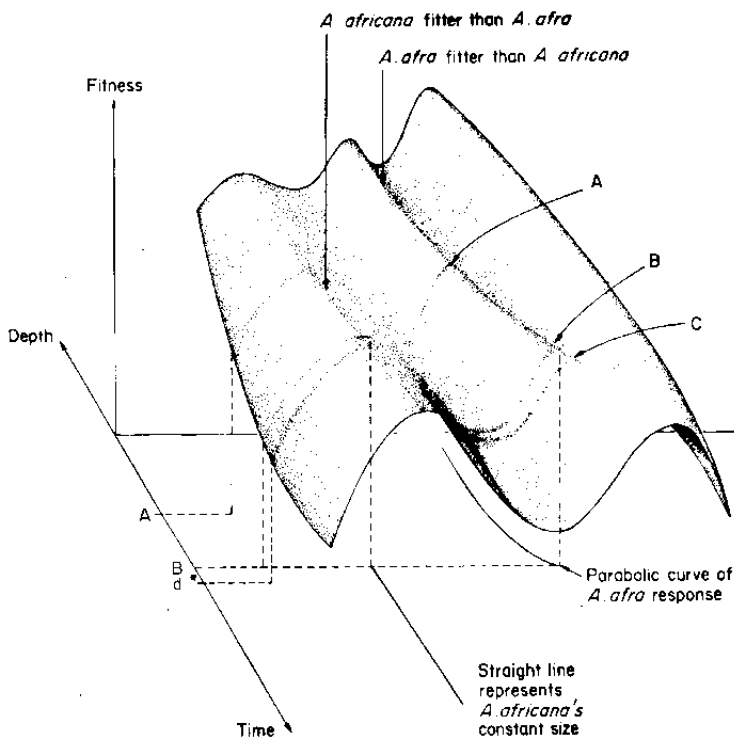


Figure 12. The change in the fitness curve of *Afrobolivina afra* at Gkebebo 1 with the change in environment parametrized by depth or time. For graphical convenience, the phenotype  $p$  is taken to be one-dimensional and is denoted by size; the phenotype could be taken to be one of the variables selected for measurement. The two lines in the plane of size and depth below the surface show the variation in the sizes of *A. afra* (curved line) and *A. africana* (straight line). Each borehole depth corresponds to a particular environment and below the threshold  $d^*$ , the fitness curve has three peaks, two corresponding to *A. afra* and *A. africana*, as shown, and two intervening minima. As the environment changed during the regressive phase of the Campanian-Maastrichtian sedimentary cycle, the peak for *A. afra* began to decrease in height relative to that for *A. africana* and to be absorbed into the flank of the higher peak. The absorption associated with the fold catastrophe and the projection to the plane gives rise to the parabolic part near  $d^*$  of the graph of size against depth. A: *Afrobolivina africana* isolated in a coast marginal environment (partly chemical sedimentation) fitter than *A. afra*. B: *A. afra* at depth 2882 ft (equivalent palaeobathymetrically to a decrease in water depth) eliminated by *A. africana* following on invasion of *afra*'s habitat by latter. C: At threshold depth  $d^*$ , the fitness peak coalesces with adjacent fitness minimum and is absorbed into the side of a higher peak.

that as the fitness peak corresponding to *A. afra* approaches a higher peak to be absorbed at threshold depth  $d^*$  (or, in other words, as the limit  $d^*$  of *A. afra*'s adaptive stability range is approached), the phenotype of *A. afra* will change parabolically (Dodson, 1975; Section 10). More precisely, for depths  $d$  just greater than the limit of the stability range or threshold depth  $d^*$ , a square-root law of the form

$$\sum_{i=1}^n a_i(p_i^* - p_i) = (d - d^*)^{1/2}, \quad (1)$$

where  $p^* = (p_1^*, \dots, p_n^*)$  is the phenotype at  $d^*$  and the  $a_i$ 's are constants, should hold. Alternatively, if  $p_j$  is a suddenly changing (or essential) character which we suppose to be increasing, then for depths greater than the threshold depth  $d^*$ , the equation

$$p_j^* - p_j = K_j(d - d^*)^{1/2}, \quad (2)$$

where  $K_j$  is a positive constant, should hold. These two equations should be compared with (2) and (3).

It is convenient for experimental purposes to take the logarithms of both sides so that the linear equation

$$\ln(p_j^* - p_j) = \ln K_j + 1/2 \ln(d - d^*)$$

should hold. We note that in Figure 12, the path of the fitness peak in the  $(d, p)$  plane should be parabolic at depths  $d$  just below  $d^*$ , i.e., an equation like (5) should hold. In the vicinity of the threshold at  $d^*$ , inessential variables will be constant or will change approximately linearly; the double log plot of the latter will have slope 1.

## 7. Extinction behaviour of *A. afra*

The analysis of the borehole data will now be continued in the light of the discussion of Sections 5 and 6. The main statistical features of the data were presented in Section 3. In the present section we view the behaviour of the species on approaching its extinction.

The variables 6 and 8 of *A. afra* (cf. Figure 2) which remain approximately constant on approaching the point of extinction (cf. p. 149) can be viewed as inessential in the sense introduced in Section 5. The approximate parabolic increase in the higher levels in the other variables is consistent with these variables being essential (again, in the sense of Section 5). Hence, the data presented here can be explained by the fitness peak of *A. afra* being absorbed into a higher peak and the intervening fitness minimum, which would have prevented the evolution of *A. afra* to a larger form, being reduced (see Figure 12). In other words, it appears that *A. afra* was approaching the limit of its stability range because of increasing environmental stress or that *A. afra* was undergoing the first phase of an adaptive form of quantum evolution associated with the fold catastrophe (Dodson, 1975).

Fortunately, we have the physical logs of the Gbekebo borehole. Evidence for an environmental trend is provided by the normal electrical resistivity log which can be used as an indicator of the environment in transgressive-regressive situations (Pirson, 1977). Further evidence of the environmental trending is yielded by the depth plot of the canonical variate means (Figure 7), which tie up well with the electrical curve (Figure 8). The environmental trend is consistent with the fitness being parametrized by borehole depth (or by time).

As is indicated by Figure 12, the critical set (i.e. the values of the environment and phenotype for which the fitness is either a peak or a saddle—naturally, for a population in stable equilibrium with its environment or, equivalently, at an adaptive peak, only the peaks are of significance) associated with the fold catastrophe is a smooth curve which does not intersect itself and which does not bifurcate or split. Consequently, adaptive sympatric speciation or splitting should not occur with *A. afra*.

Little can be said about the morphology outside the stability range or above the threshold depth apart from its continuing to change in the same direction as the parabolic change. Thus, if the ancestral form is increasing up to the threshold, as is the case with *A. afra*, the descendent form should also increase until it reaches a new adaptive peak. If we now look at the situation pertaining around the Cretaceous-Tertiary transition in western Nigeria, there is only one known related species, *A. africana*. As a result of the foregoing argument, the smaller *A. africana* cannot have evolved from *A. afra* in western Nigeria by means of adaptive quantum evolution. This conclusion is a consequence of the assumptions that the evolutionary process is adaptive, the population canalized with limited phenotypic variation and

that the fitness is smooth. It does not depend on Thom's theory which gives the extra information that the phenotypic response of the ancestral population prior to the threshold should be parabolic.

These ideas have been discussed in more detail in connexion with sudden and irreversible changes in phenotype associated with a threshold (i.e. quantum evolution) occurring in an homogeneous, canalized and adaptive population in a uniform and slowly varying environment (Dodson, 1975).

### 8. The succession of *A. africana*

At the time of *A. afra*'s replacement by *A. africana*, the environment appears to have been gradually changing, though homogeneous and uniform. In none of the many samples examined have *A. afra* and *A. africana* been found together, nor have any specimens been seen that could be passage or intermediate forms between the two species. The same observation applies to Cameroun and, seemingly, also to Gabon.

There is some evidence, however, that their ranges overlap slightly. *A. afra* passes into the Paleocene (Danian) in Nigeria and possibly also in Gabon (Reymont, 1963; 1966a; 1966b). *A. africana* seems to have lived in shallow water, while *A. afra* preferred a somewhat deeper environment. Also, the former occurs in calcareous sediment, the latter in clay-shales.

There is no evidence of a major geographical barrier between Akisinde, Araromi, Afowo, and Gbekebo. Akisinde and Afowo lie in the Dahomey embayment of the Nigerian coastal sedimentary basin which was never cut off from the main sedimentary basin at any time in the Late Cretaceous through to the Paleocene.

In the present study, there does not appear to be any satisfactory way of explaining the morphometric passage from *A. afra* to *A. africana* (if one were to assume that the latter gave rise to the former) in terms of a sympatric model of speciation.

The absence of intermediate forms excludes an adaptive model for quantum evolution for the whole of this evolutionary event (Dodson, 1975). This, and the conditions at the time, suggest that the replacement of *A. afra* by *A. africana* could be explained by the adaptive evolutive model of Dodson & Hallam (1977) for allopatric speciation. According to this model, the observed parabolic increase in the size of *A. afra* prior to its disappearance leads to a larger descendant. Since *A. africana* is substantially smaller, the model cannot apply.

In consequence of the foregoing, *A. africana* cannot be the direct descendant of *A. afra* without the intervention of some heterogeneity or discontinuity in the environment or some evolutionary process such as saltation or splitting from a common ancestor. This suggests that the frequently observed occurrence of a species being replaced by a significantly smaller form may not be a straightforward process (Hallam, 1978).

Now, it has been shown that the conformity with a parabola of the secular size increase of *A. afra* on approaching its extinction is consistent with the absorption of its fitness peak into the flank of a higher peak. Thus, as has been argued, this part of the speciation event in which *A. afra* was replaced by *A. africana*, can be described in terms of the model of quantum evolution involving the fold catastrophe (Dodson, 1975). In this case, *A. africana* cannot have evolved sympatrically from *A. afra* in central western Nigeria. Also, it would follow from the absence of a larger descendant that *A. afra* was replaced by *A. africana* before the peak was absorbed, i.e., before the threshold for quantum evolution had been attained. In other words, under the set of ecological conditions pertaining in early Paleocene time, *A. africana*

that the fitness is smooth. It does not depend on Thom theory which gives the extra information that the phenotype response of the ancestral population prior to the threshold should be parabolic.

These ideas have been discussed in more detail in connexion with sudden and irreversible changes in phenotype associated with a threshold (i.e. quantum evolution) occurring in an homogeneous, canalized and adaptive population in a uniform and slowly varying environment (Dodson, 1975).

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was fitter than *A. afra* and was able to invade its range before *A. afra* underwent quantum evolution (Figure 12).

The replacement of the one species by the other can be viewed in relation to the long-term environmental shift caused by the eustatic fall in sea-level associated with the regressive phase of the Maastrichtian sedimentary cycle. Thus, assuming that the process was adaptive, the change in the environment due to the falling sea-level caused the fitness peak corresponding to *A. afra* to begin to coalesce into the flank of a higher peak corresponding to a larger stable form. In addition, the changing environment had the effect of lowering the height of the fitness function in the vicinity of the peak corresponding to *A. afra* to below that of the peak corresponding to *A. africana*, or, equivalently, to raising the latter above the former.

The variation in the immediate vicinity of Gbekebo of the fitness arising from the secular environmental change can be represented by the surface of changing fitness curves drawn in Figure 12.

The regressive phase of the Maastrichtian sedimentary cycle would tend to lead to a reduction in the homogeneity of the coastal environment, facilitating the isolation of sub-populations and increasing the likelihood for speciation events. When these shallow regions of highly stressed and variable environment were flooded during the following transgressive phase of the Paleocene sedimentary cycle, any fitter species which had evolved would have been able to spread and compete effectively with other forms (Hallam, 1978; p. 23). Note that the heterogeneous and fluctuating coastal environment is excluded from the model of Dodson & Hallam (1977). There is also evidence that in shallow seas, with their highly stressed environments and increased danger of extinction, *r*-selection is the dominant adaptive strategy (cf. Gould, 1977; p. 310), leading to smaller organisms. This interpretation would therefore account for *A. africana* being smaller than *A. afra*, since in contrast, deeper waters are normally associated with low environmental stress, with *K*-selection as the dominant adaptive strategy and a phyletic size increase as a consequence (Hallam, 1978; pp. 20–21).

There are other possible explanations for the smaller size of *A. africana* in relation to *A. afra* that are also plausible. One possibility is that the fitness peaks are very shallow and that there is a substantial spread of phenotypes in the population. Under such circumstances, a slight tilt of the fitness function could have the effect of reversing the direction of evolution (Figure 13). This tilting would have to have occurred before the threshold and in an area away from that of the boreholes, as there is no sign of the continuous reversal in size of stable forms that such an explanation implies. Another possibility is for the presumptive peak, into which the fitness peak corresponding to *A. afra* is absorbed, to be absorbed in turn into

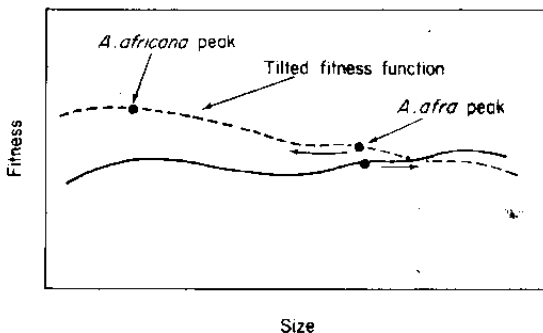


Figure 13. A graph of the fitness plotted against size when the fitness peaks are very shallow. A slight tilt, indicated by the dotted curve, reverses the direction of evolution, which proceeds upwards.

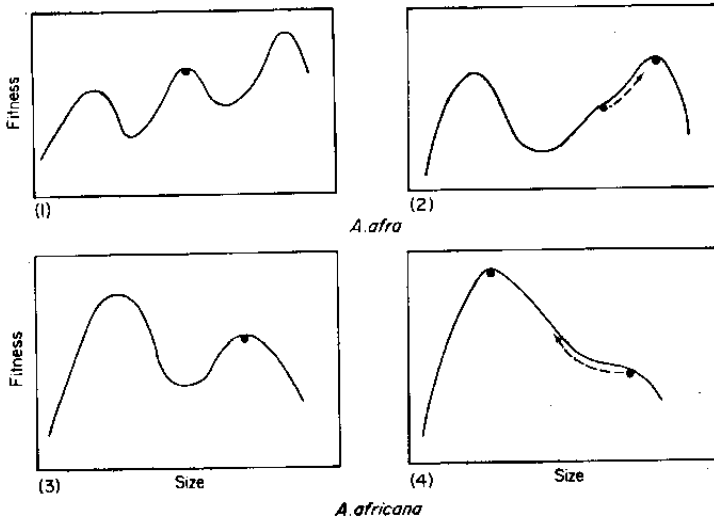


Figure 14. A sequence of graphs of the fitness against size for differing environments. The heavy dots mark the peak determining the size. In 1, the heavy dot represents the phenotype of *A. afra* at a fitness peak. In 2, the middle peak corresponding to *A. afra* is being absorbed into the flank of the right hand peak, giving rise to quantum evolution and a parabolic increase in size. In 3, the middle peak has been absorbed. In 4, the right hand peak is absorbed into the flank of the peak for *A. africana*, bringing about quantum evolution and a parabolic decrease in size up to the threshold.

the flank of the fitness peak corresponding to *A. africana*, with a parabolic size decrease prior to the threshold (Figure 14). Again, this would have to take place away from the area of the boreholes and in shallower waters further in the direction of the environmental gradient. A third possibility is that the fitness function changes with the environment in such a way as to cause the size to decrease, for instance, by moving to the left in Figure 14. This is, however, excluded by the assumption that the environment (hence the fitness) is varying sufficiently slowly. This assumption, or others, such as the limited phenotypic variation, could, of course, be wrong, but we believe that the explanation involving the initial phase of quantum evolution and allopatric speciation in coastal waters provides a reasonably satisfactory vehicle for interpreting the observed features of the extinction of *A. afra* and its replacement by *A. africana*.

## 9. Conclusions

The unexpected increase in size of *Afrolivina afra* before its extinction implies that its replacement by the smaller *A. africana* is not a direct, local succession. The succession by a smaller form can be explained by the different selective modes which can operate in deeper homogeneous waters (unstressed environment) and the shallower littoral regions (stressed environments), as interpreted by Hallam (1978). The approximate conformity with a parabolic or square-root law shown by many morphological characters of *A. afra* prior to extinction is evidence, though we emphasize, not conclusive evidence, that the fitness peak of *A. afra* was being absorbed into the flank of a higher peak. A parabolic increase in size of *A. afra* can be thought of in terms of supplying quantitative evidence for Thom's ideas of morphogenesis and, consequently, as possible support for the biological concepts to which Thom theory is applied. To take the matter a step further, a parabolic

increase in size also provides quantitative evidence for the validity of the Simpson-Wright selection landscape concept, or fitness surface, and for the neo-Darwinian thesis that despite the discrete nature of individual Mendelian mutations, the evolutionary process can be considered to be continuous at a population level.

The fossil record for micro-organisms is a promising source of material for quantitative evolutionary analyses, although the data presented here are not complete enough in the crucial region in the vicinity of extinction to yield conclusive evidence for a parabolic phenotypic response. Thus, we suggest that data from boreholes through unbroken sedimentary sequences be examined closely in the neighbourhood of the extinction or replacement of species of micro-organisms. We appreciate the difficulties involved, especially since the critical region near a threshold need not be large; nevertheless, we believe that such a programme would be worth pursuing.

### Acknowledgements

We are grateful to Professor A. Hallam and Dr R. E. Blackith for kindly commenting on an early draft of the paper and to a referee for making useful suggestions concerning the manner of presenting our results. We wish to thank Gustav Andersson, Dagmar Engström and Eric Ståhl, Uppsala, for the illustrations and Eva Reymont for the painstaking SEM work and the measuring of the material. Uppsala University provided computing funds and Reymont's research was sponsored by a grant from the Swedish Board for Technical Development (STU).

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