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THRESHOLD CHARACTERS IN A CRETACEOUS FORAMINIFER

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ABSTRACT

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A threshold character is one for which the phenotypic values are discontinuous but the mode of inheritance is like that of a continuously varying character. The appearance of such characters may be connected with an environmental stimulus. The Cretaceous bolivinid *Afrobolivina afra* produced three ornamental variants which appear to represent true threshold characters; these were possibly under the control of water-depth.

INTRODUCTION

In quantitative genetics, the occurrence of multifactorial characters has long been known. The phenotypic development of such characters may be expressed, for example, in the presence or absence of an organ, resistance to disease, etc. Among invertebrates, species of the banana fly (genus *Drosophila*) have been most closely studied.

The usual methods of quantitative genetics cannot be applied to the analysis of threshold characters. However, Falconer (1960) and Rendel (1967) have pointed out that such characters are under the influence of many genes, just as any metric character. Grüneberg (1952) introduced the concept of quasi-continuous variation for threshold characters in his work on mice. Here, the phenotypic values are discontinuous but the mode of inheritance is like that of a continuously varying character.

Quasicontinuous variation has been extensively studied by Rendel (1967, 1979) and Falconer (1960, Chapter 18) provides detailed notes on the statistical methods used for analyzing threshold characters.

It is known that a threshold character may appear as the result of the influence of an environmental stimulus. Selection may eventually cause such a character to appear spontaneously without the intervention of the environmental factor that first triggered its appearance (Falconer, 1960, p. 310). In the present case, there seems to be reasonable evidence for the environmental control of the occurrence of the ornamental varieties.

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THRESHOLD CHARACTERS IN *AFROBOLIVINA*

Afrobolivina afra Reyment (Late Campanian to Danian) produced three ornamental variants, one showing a reticulated pattern of ribbing with flattened and thickened sutures (denoted *re* in the following), a longitudinally ribbed variety (here denoted *co*), and a mainly smooth morph with weakly developed sutures (denoted *sm* in the following). These three ornamental variants commonly, but not invariably, occur in one and the same sample and they are distributed throughout the geographical range of the species. Examples are illustrated in Plate I. The costate phenotype is shown in Plate I, a, b, and c (from borehole depths 895, 898 and 916 m). The reticulate phenotype is illustrated in Plate I, d, e, f and g (from borehole depths 906, 912, 970 and 1020 m). The lobate, smooth phenotype is shown in Plate I, h, i and j (borehole depths 970, 916 and 912 m). All specimens are from a borehole drilled at Gbekebo, coastal western Nigeria.

QUANTITATIVE GENETIC ANALYSIS OF THRESHOLD CHARACTERS

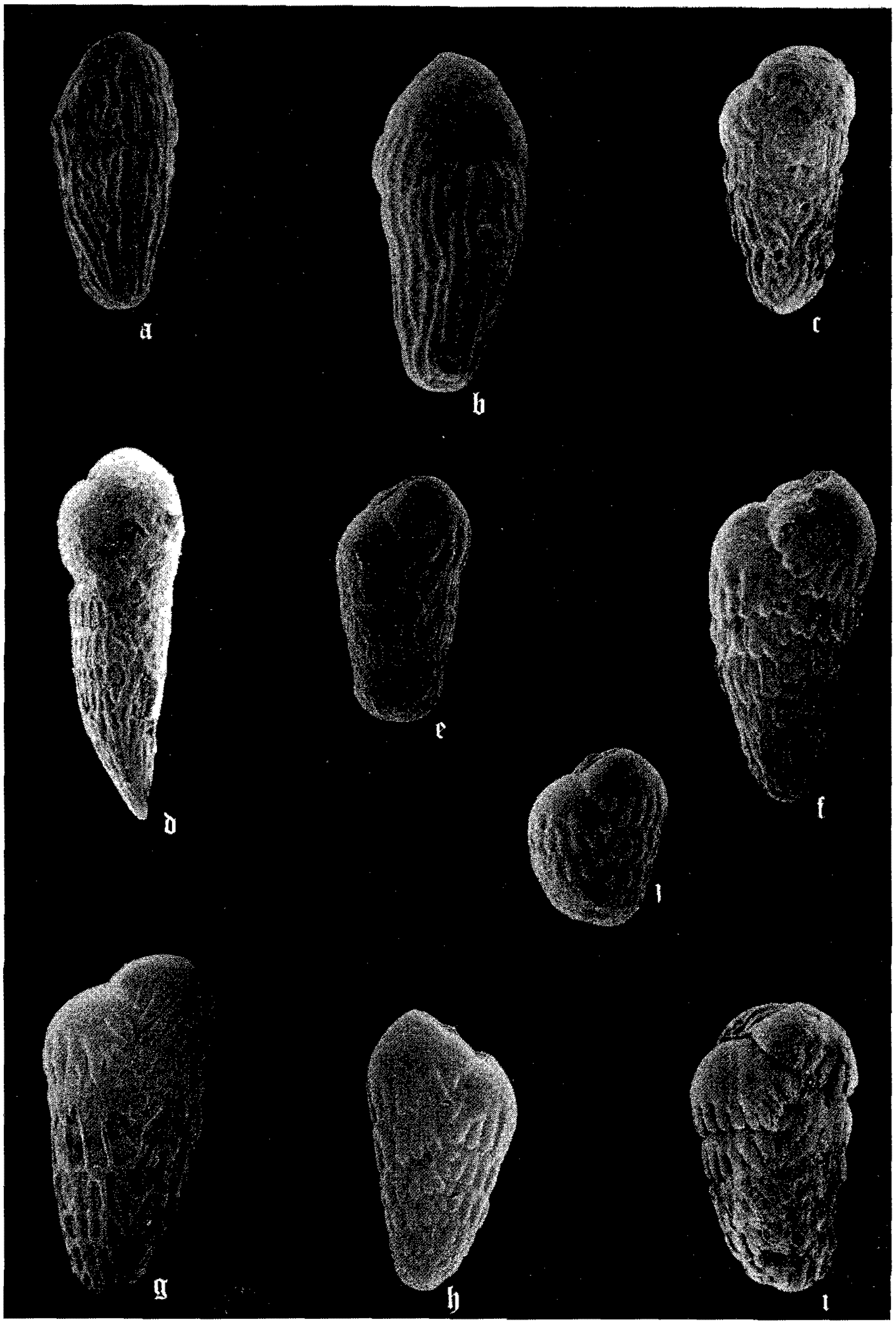
In analyzing quasi-continuous variations, it is assumed that such a character has an underlying continuity with a threshold which manifests itself in the visual expression of the character. The underlying continuous variation is of genetic and environmental origin. The hypothetical measurement of this variation must be made on a scale that makes its distribution normal, the standard deviation of the distribution being the unit of measurement. This constitutes the underlying scale. This scale is joined to the visible, discontinuous scale by the threshold, that is, the point of ornamental discontinuity. Clearly, on the visible scale, individuals can only have two possible values, 0 or 1. Thus, individuals whose phenotypic values on the underlying scale exceed the threshold will appear in one visible class, while those with values falling below the threshold will appear in the other. An example of the relationship involved is given in Fig.1 for *A. afra*. Here the thresholds for the ornamental variants occur at 0 and 1 on the underlying scale; i.e., one of the thresholds (*sm/co*) lies at the origin and the difference between this and the second threshold (*co/re*) is the unit of measurement — one threshold unit.

If the three frequencies are *sm* = 20%, *co* = 15% and *re* = 65%, the deviations of the thresholds from the population mean are found as follows from a table of the normal curve:

PLATE I

Examples of the three morphs of *Afrobolivina afra*. The costate variant: a (895 m), b (898 m), c (916 m). The reticulate variant: d (906 m), e (912 m), f (970 m), g (1020 m). The smooth variant: h (970 m), i (916 m), j (912 m). All figures are magnified about 35 times except d, a large microspheric individual, which is magnified about 25 times.

PLATE I



deviation. This permits us to examine a sequence of samples for evolutionary changes in the character of interest.

Nine samples selected from the available stratigraphical range of the species in the Gbekebo borehole, and one from the nearby Araromi borehole, were analyzed by the procedures given in Falconer (1960) and exemplified above. The results are summarized in Table I and Fig.2. All but one of the standard deviations are compatible. The means increase through time until the final level, where there is a sudden fall-off. The trend displayed by the threshold mean in Fig.2 shows a remarkable agreement with the transgressional history of western Nigeria. The first eight levels derive from sediments deposited during the Late Maastrichtian regression, whereas the youngest sample is from the strongly transgressive Danian (Paleocene). This relationship could possibly reflect the weakening of an environmental stimulus (here, presumably depth of water), that is, the reverse mechanism to "genetic assimilation", whereby an environmental factor can bring about the appearance of a variant (Falconer, 1960). There is a gradual loss of the reticulate morph (Table I) and a roughly corresponding increase in the frequency of the costate morph.

It will be seen from Table I that the occurrence of the morphological classes possesses regional validity (cf. samples 3 and 10, which are geographically separated) as well as temporal validity.

TABLE I

Frequencies, means and standard deviations in threshold units for the three ornamental classes

Location	Sample No.	Depth (m)	Incidence			Deviations of thresholds from mean in σ		Means and standard deviations in threshold units	
			re	*sm*	*co*	*re/sm*	*sm/co*	M	$\hat{\sigma}$
Gbekebo	1	351	90	5	5	+1.28	+1.65	−3.46	2.70
	2	305	43	34	23	−0.18	+0.74	0.20	1.09
	3	255	37	31	31	−0.33	+0.47	0.41	1.25
	4	221	5	57	38	−1.64	+0.31	0.84	0.51
	5	171	2	46	56	−2.05	−0.05	1.03	0.50
	6	121	1	15	84	−2.34	−0.99	1.73	0.74
	7	42	1	7	92	−2.34	−1.40	1.73	1.06
	8	15	18	5	77	−0.92	−0.74	5.15	5.60
	9	0	12	54	34	−1.18	+0.41	0.74	0.63
Araromi	10		34	32	33	−0.38	+0.44	0.46	1.22

The chronological order of the Gbekebo samples is from 1 (oldest) to 9 (youngest). Samples 1 through 8 and 10 are of Late Maastrichtian age. Sample 9 is Early Paleocene (Danian).

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from *A. afra* through an allopatric speciation event (Dodson and Reyment, 1980), also shows threshold variation, judging from Ogbe's descriptions, and cannot represent "phylogenetic developments".

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