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Speciation and structural evolution in the Palaeocene *Morozovella* lineage (planktonic Foraminiferida)

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ABSTRACT – The Palaeocene members of the planktonic foraminiferal genus *Morozovella* evolve through a series of intermediate morphologies from the globigerine ancestral species *Subbotina pseudobulloides* to the angulo-conical globorotaliid species *Morozovella velascoensis*. This example of structural evolution is investigated using eigenshape analysis on 41 samples from DSDP Site 577 (Shatsky Rise, North-West Pacific). The results indicate that the initial members of this lineage *(S. pseudobulloides* to *M. angulata* forma *protocarina)* exhibit a directional shape trend whereas, subsequent to the evolution of *M. velascoensis*, shape fluctuations are random. The interval of maximum shape change in this lineage is accompanied by an increase in the mean size of its members. Both the shape and size change occur during the peak in speciation of the Palaeocene morozovellids (at 63Ma), a phenomenon that we interpret as an example of species selection. This interval is also characterised by high levels of marine productivity, a factor considered instrumental in the control of the evolution of the Palaeocene *Morozovella* species.

The potential of eigenshape analysis as a taxonomic aid is also investigated. Specimens mounted in side view are insignificantly different until the evolution of the late stage morozovellids *M. angulata* forma *protocarina, M. velascoensis, M. occlusa* and *M. edgari* in the Late Palaeocene. This suggests that the shape of the edge view of Palaeocene morozovellids is not a good measure of real species differences.

INTRODUCTION

The distinction between phylogenetic and taxonomic rates of evolution dates back to the pioneering work of Simpson (1953). Phylogenetic evolution is the name given to the evolution of a character or set of characters in a lineage whereas taxonomic evolution considers changes in the rate of origination and extinction within faunas or floras. The study of the different types of evolutionary pattern requires the employment of different methods of measurement. In the case of phylogenetic or structural evolution within a lineage, it is clear that the requirement is to measure shape change or some related parameter. Measurement of the species diversity of Palaeocene planktonic foraminifera, and their rate of origination and extinction has been discussed by Corfield (1987a) in the context of the isotopically heavy values of $\delta^{13}C$ that characterise the Late Palaeocene.

In this contribution, the structural evolution of the Palaeocene members of the genus *Morozovella* is considered. This genus of planktonic foraminifera became a distinct faunal component of low and mid latitudes two million years after the Cretaceous /Tertiary boundary extinctions and represents the first step in the re-establishment of relatively complex planktonic foraminiferal morphologies such as characterised the faunas of the Late Cretaceous.

The succession of Palaeocene morozovellids has been considered by many authors (e.g. Subbotina, 1953; Bolli, 1957; Loeblich & Tappan, 1957; Berggren, 1968; Toumarakine & Luterbacher, 1985; Corfield, 1987a and unpublished thesis) largely because of the biostratigraphic importance of this genus (see, for example, Berggren *et al.*, 1985). The important evolutionary trends in this genus are:

(1) The development of an angulo-conical test from a globigeriniform ancestor.
(2) The acquisition of a peripheral test muricocarina (the pseudokeel).
(3) The development of muricae upon the surface of the test. These features, together with the species that first exhibit them, are illustrated in Fig. 1 and Pl.1.

The assignment of the morozovellid ancestral species *pseudobulloides* to the genus *Subbotina* reflects the origin of the genus *Morozovella* in the primitive globigeriniform planktonic foraminifera of the Early Palaeocene. These early forms do not possess any of the features by which the later morozovellids are recognised. We have not analysed these Danian planktonic foraminifera for, at the time this study was performed, samples of this age were unavailable to us.

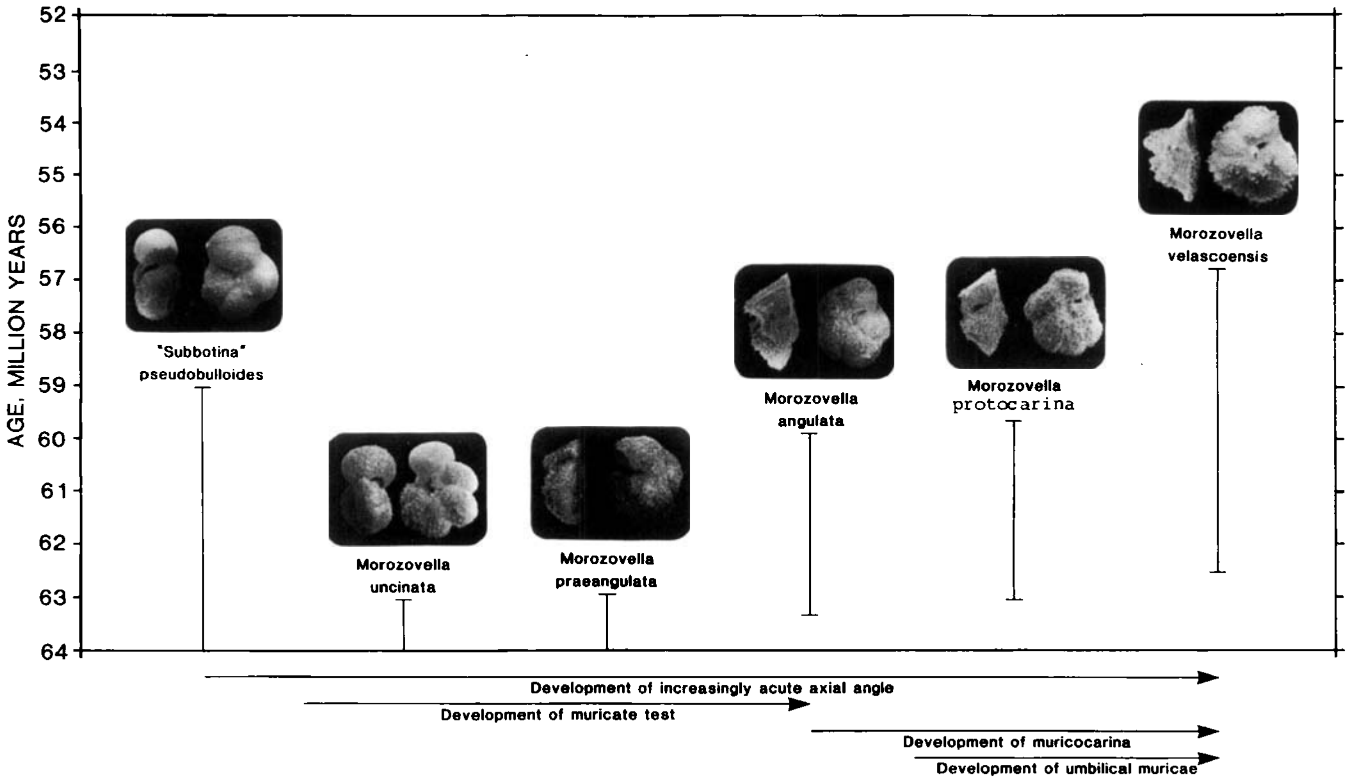

Fig. 1. Morphological developments in the Palaeocene *Morozovella* lineage (modified after Corfield, 1987a).

It is clear from Fig. 1 that the members of this genus do not provide an example of phyletic gradualism – the gradual transformation from ancestor to descendant states without overlap of component species – (Eldredge & Gould, 1972) since the attainment of the three characters that are a feature of the genus *Morozovella* occurs as a result of speciation, superimposed on a directional shape transformation.

The study of the structural evolution of the Palaeocene *Morozovella* lineage is well supported by the new understanding that is developing of environmental events during this period (Shackleton, 1986a). In particular the anomalously heavy values of ^{13}C in micro- and nannofossil carbonate at this time suggest a major increase in ocean productivity (Shackleton, 1986a, 1987). The possible effect of this event on patterns of taxonomic evolution has been discussed by Corfield (1987a).

The aims of this morphometric study are twofold: (1) To assess the importance of the shape of the edge view in identifying species of the genus *Morozovella* (MORTEST analyses).

(2) To morphometrically quantify the phylogenetic development of the Palaeocene *Morozovella* lineage and assess the rate and nature of evolutionary shape change through the Palaeocene (MOROZ and MOROZALL analyses).

SYSTEMATIC PALAEONTOLOGY

In the following account, Pl. 1 illustrates the important members of the Palaeocene *Morozovella* species.

The first species that can be clearly identified as ancestral to the Palaeocene morozovellids is the species *S. pseudobulloides,* which possesses a globigeriniform morphology (Pl. 1, figs, 1, 2), while the final product of this evolutionary sequence is *M. velascoensis,* the type species of the genus (Pl. 1, figs 13, 14). This species shows the features that are considered typical of the group, that is the acute axial periphery which bears a keel composed of closely appressed muricae (the muricocarina of Blow, 1979), together with the pronounced angulo-conical test shape.

The two are separated by several morphologically intermediate species that show progressive develop-

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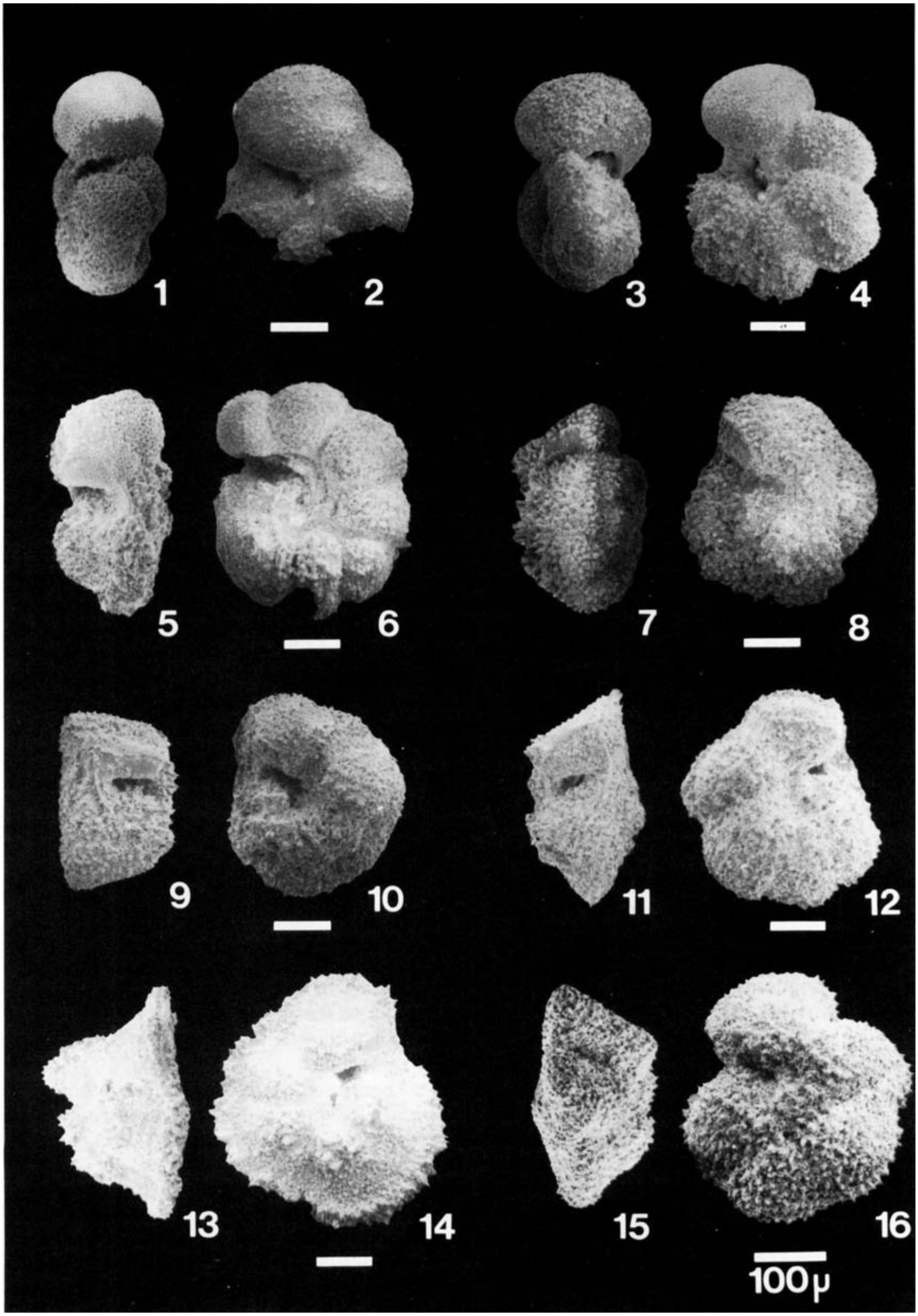
Explanation of Plate 1

Some important species within the Palaeocene *Morozovella* lineage.

Figs. 1, 2, *Subbotina pseudobulloides;* figs. 3, 4, *Morozovella uncinata;* figs. 5, 6, *Morozovella praecursoria;* figs. 7,8, *Morozovella praeangulata;* figs. 9, 10, *Morozovella conicotruncata;* figs. 11, 12, *Morozovella angulata* forma *protocarina;* figs. 13, 14, *Morozovella velascoensis;* figs. 15, 16, *Morozovella angulata.*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ment of the characteristics of the type species. Because of this, it is useful to divide the Palaeocene morozovellids into three groups based on their relative morphological organisation.

Primitive morozovellids are *S. pseudobulloides, M. trinidadensis, M. praecursoria* (Pl. 1, figs. 5, 6) and *M. uncinata* (Pl. 1, figs. 3, 4).

Intermediate morozovellids are *M. praeangulata* (Pl. 1, figs. 7, 8), *M. angulata* (Pl. 1, figs. 15, 16), *M. conicotruncata* (Pl. 1, figs. 9, 10) and *M. angulata* forma *protocarina* (Pl. 1, figs. 11, 12).

M. angulata forma *protocarina* is distinguished from *M. angulata* s.s by virtue of its possession of a muricocarina and partially developed umbilical muricae. White's (1928) illustration of the holotype of *M. angulata* does not show these features.

Blow (1979, pp. 984–985) suggested that the *angulata* concept encompasses forms from this unkeeled, naked shouldered morphotype through to phylogenetically advanced specimens with a primitive keel and some umbilical murical development. It is this that we call forma *protocarina.* Corfield (1987a) originally designated this morphotype *praevelascoensis*, but to avoid a proliferation of 'prae' prefixes in micropalaeontology, we now prefer the more descriptive term 'protocarina' (proto=first; carina=keel).

It may be that the form *protocarina* deserves separate specific status; this question has been addressed by Corfield & Shackleton (in prep. a).

Late stage morozovellids are *M. velascoensis, M. occlusa,* and *M. edgari.*

There is at present some debate among workers in the field as to the number of lineages represented by the Palaeocene morozovellids. Thus Toumarkine & Luterbacher (1985) believe that there are two parallel lineages that show the progressive development of late Palaeocene morozovellid features, while Boersma & Premoli-Silva (1983) suggest that there may be as many as three lineages involved. The approach of the present study is to treat this sequence of forms as one lineage pending further information. This information is likely to be forthcoming from the recently formed International Working Group on Palaeogene Planktonic Foraminifera.

MORPHOMETRY

Morphometry is the quantitative study of the morphology of both living and fossil organisms. A characteristic of this science is that it routinely demands the acquisition and processing of large amounts of measurement data. It is this, more than anything else, that has limited the widespread application of this technique in the past, for the data collection when performed by eye becomes rapidly tedious (especially when dealing with microscopic organisms) and the statistics required to reduce a large, multivariate data set are not easily performed without the aid of computers. This has not, however, prevented pioneering studies from being made, e.g. Hallam & Gould (1975) on *Gryphaea,* and Malmgren (1974) on *Subbotina pseudobulloides.* However, in recent years the development of microprocessor controlled video-digitizers has speeded the process of data collection considerably and this advance, taken together with the enormous data processing capability of computers, has allowed more detailed studies of the morphology of organisms than was previously possible.

METHODS

Forty-one samples from the Palaeocene of Deep Sea Drilling Project Site 577 on the Shatsky Rise in the North Pacific 32° 26.51′, 157° 43.40′) were selected for this analysis. Core and sample numbers., together with depth, estimated ages and component species are given in Table 1. Age estimates are given here to two decimal places. Although the absolute ages of sample levels are likely to change with refinements to the geological timescale, the relative lengths of intervals between samples are not, and it is therefore valuable to employ such a fine temporal resolution for the purposes of this study.

The Palaeocene timescale used in this study was developed using the age estimates for datums listed in the magnetobiochronology of Berggren *et al.* (1985). Age estimates for magnetic reversals were derived from the published magnetostratigraphy (Bleil, 1985) and the reversals were identified using the nannofossil zonation of Monechi (1985) and unpublished data (Shackleton, pers. comm.). The techniques used for the development of this timescale are fully described by Corfield (Unpub. PhD thesis), and Corfield & Shackleton (in prep. b). Site 577 was selected for this study because of the excellent preservation of planktonic foraminifera during the Palaeocene and the fact that it was drilled using the hydraulic piston corer, a feature that enhances the potential stratigraphic resolution. Members of the genus *Morozovella* are low latitude species so the position of Site 577 at approximately 14° N (Firstbrook *et al.*, 1979) during this interval is also advantageous.

Approximately 50 specimens from each sample were picked from the >150µm fraction and mounted in edge view on double sided tape attached to a normal microscope slide. The choice of specimens was random so that varied ontogenetic stages and morphologies within a species concept were selected. The edge view orientation was selected since the two major features of the morozovellid structural development (increasing anguloconicality, and the development of the pseudokeel) are most easily seen in this orientation. However, in order to investigate the importance of the umbilical orientation for a more refined, future study, one sample was mounted in umbilical view (MORTESTUMB).

Scott (1980) has shown that the outline of a planktonic foraminiferan contains a great deal of information and contributes much to the species discriminating ability of a micropalaeontologist. Hence, while recognising the wealth of information available from a classical study of selected linear dimensions of the test (e.g. Malmgren & Kennett, 1981; Backman & Hermelin, 1986), it was the outline images of the tests that were collected for this study.

The measurements were collected and analysed using the Micro-computer based Image Analysis System (MIAS) at the University of Stockholm (Granlund & Hermelin, 1984).

Table 1. Samples analysed with depths and estimated ages from DSDP Sites 577 and 577A. An asterisk indicates a sample from DSDP 577A, otherwise all samples are from DSDP 577.

	Sample	Depth (m)	Age (Ma)	N	Species
1)	9/6/120	82.0	56.77	51	*M. velascoensis*
2)	10/1/ 60	83.4	57.82	58	*M. velascoensis*
3)	10/1/120	84.0	58.06	51	*M. velascoensis*
4)	10/2/ 60	84.9	58.42	50	*M. velascoensis*
5)	10/2/120	85.5	58.65	50	*M. velascoensis*
6)	10/3/ 60	86.4	58.89	55	*M. velascoensis*
7)	10/3/120	87.0	59.06	53	*M. velascoensis*
8)	10/4/ 30	87.6	59.22	65	*M. velascoensis*
9)	10/4/ 90	88.2	59.34	67	*M. velascoensis*
10)	10/5/ 0	88.8	59.44	61	*M. velascoensis*
11)	10/5/ 60	89.4	59.55	61	*M. velascoensis*
12)	10/5/120	90.0	59.66	56	*M. velascoensis*
13)	10/6/ 30	90.6	59.77	56	*M. velascoensis*
14)	10/6/ 90	91.2	59.88	55	*M. velascoensis*
15)	11/1/ 0	92.3	60.08	56	*M. velascoensis*
16)	11/1/ 60	92.9	60.20	55	*M. vel/M. proto*
17)	11/1/120	93.5	60.32	55	*M. vel/M. proto*
18)	11/2/ 60	94.4	60.50	70	*M. vel/M. proto*
19)	11/3/ 0	95.3	60.52	64	*M. vel/M. proto*
20)	10/5/129*	92.7	60.22	60	*M. vel/M. proto*
21)	10/6/ 34*	93.2	60.32	55	*M. vel/M. proto*
22)	11/1/ 30*	95.2	61.86	57	*M. proto/M. ang*
23)	11/3/120	96.5	61.68	50	*M. protocarina*
24)	11/1/ 90*	95.8	61.98	48	*M. proto/M. ang*
25)	11/2/ 0*	96.4	62.10	54	*M. ang/M. praea*
26)	11/2/ 90*	97.3	62.29	63	*M. ang/M. praea*
27)	11/3/ 59*	98.4	62.53	61	*M. ang/M. praea*
28)	11/4/ 0*	99.4	62.71	63	*M. ang/M. praea*
29)	11/4/ 60*	100.0	62.83	61	*M. praeangulata*
30)	11/5/ 0*	100.9	63.02	72	*M. praeangulata*
31)	11/5/ 28*	101.2	63.14	56	*M. praea/M. pcr*
32)	11/5/ 59*	101.5	63.30	55	*M. praea/M. pcr*
33)	11/5/ 90*	101.8	63.46	63	*M. praea/M. pcr*
34)	11/5/120*	102.1	63.57	69	*M. praeangulata*
35)	11/6/ 0*	102.4	63.63	54	*M. praea/M. pcr*
36)	11/6/ 30*	102.7	63.69	58	*M. praecursoria*
37)	11/6/ 59*	103.0	63.75	70	*M. trinidadensis*
38)	11/6/ 90*	103.3	63.82	60	*M. trin/S. pseu*
39)	11/6/121*	103.6	63.88	55	*M. trin/S. pseu*
40)	11/7/ 2*	103.9	63.95	70	*S. pseudobull*
41)	11/CC/5*	104.1	64.00	50	*S. pseudobull*

M. vel = *M. velascoensis* forma *protocarina*
M. praea = *M. praeangulata*
M. trin = *M. trinidadensis*
M. proto =*M. angulata*
M. ang = *M. angulata*
M. pcr = *M. praecursoria*
S. pseu = *S. pseudobulloides*

EIGENSHAPE ANALYSIS

Eigenshape analysis consists of two components. The first of these is the collection of the outline of the shape by the computer and the subsequent interpolation to 128 straight-line segments using the Zahn & Roskies (1972) shape function. The net angular change between segments allows the computer to manipulate the shape of the microfossil quantitatively.

This function describes how a shape differs from a circle, and contains all the information necessary to reconstruct the microfossil outline. The size component of differences between shapes is also removed by the function.

It is critical to the comparability of the eigenfunctions of the shapes in a sample that each of the 128 straight line segments are homologous with the same segment in other specimens and other samples. Failing this, specimens are rotated relative to each other to the point of maximum correlation (Lohmann, 1983; Lohmann & Malmgren, 1983). At this point, segments are assumed to be homologous with each other.

It should be noted, however, that in this study it was usually possible to locate a homologous point (the tip of the final chamber) on all specimens from all samples. Hence the degree of rotation required was generally small.

The second part of eigenshape analysis is simply a principal components analysis, which uses as its input data the information from the shape function. The net result of the two components of eigenshape analysis is the quantification of the differences and similarities within a suite of shapes and the construction of a mean shape to represent a given sample.

The eigenshapes are the minimum number of these mean shapes needed to describe the shape variability within a sample (Lohmann, 1983). Hence the first eigenshape describes the axis of greatest variation in a data set in the same way as the first principal component in a principal components analysis. Successive eigenshapes describe progressively decreasing axes of variability in the data. Typically, only a few eigenshapes are required to successfully describe most of the variability in a data set. In this study three eigenshapes described 94% of the variance in all 41 samples.

Recently, the technique of eigenshape analysis has come under attack (Full & Ehrlich, 1986). There are two areas of contention: (1) the assumption of homology after rotation of the specimens to the point of maximum correlation and (2) the underlying rationale of multivariate normality implicit in the use of a principal components analysis.

Because the homologous point on the tip of the final chamber could always be located by eye in this study, criticism (1) does not apply. Addressing criticism (2), eigenshape data are likely to have a more 'normal' distribution than other shape analytical techniques, because of the comparability of data arrays collected using a similarly placed start point. In addition, nowhere in the eigenshape procedure are any statistical distributions actually used, as they are, for example, in factor analysis.

Two distinct types of information are yielded by eigenshape analysis: (1) the eigenshapes themselves which are mathematical representations of the nature of the modification required to change a circle into the eigenshapes, and (2) the amplitude of the eigenshapes, which represent the *amount* of modification necessary to distort a circle into the shape specified by the eigenshapes. The amplitude is the correlation coefficient of the observed shape with the eigenshape. Hence the amplitude is a more useful measure of shape change than the values of the eigenshapes (Lohmann & Malmgren, 1983).

Additionally, since the first eigenshape represents the mean shape of the observed forms in the sample analyses, or the first eigenshapes in the between-sample analyses, the second eigenshape is a better measure of evolutionary change because it portrays the principal dimension of shape variation around this mean (Lohmann, 1983).

Thus, it is the amplitude of the second eigenshape that is employed for the analysis of structural evolution in the Palaeocene *Morozovella* lineage.

THE DISCRIMINATION OF *MOROZOVELLA* SPECIES USING EIGENSHAPE ANALYSIS

Five tests were conducted to evaluate the potential of the eigenshape technique in aiding the species discriminating ability of micropalaeontologists. For simplicity, these tests are referred to as MORTESTS in this paper.

Ultimately, it would be valuable to be able to use this technique to assign correct species names to members of an unsorted population of foraminifera. However, at this time the necessary technology is not available. In order to approach this ideal situation, the MORTEST samples were analysed after having been sorted into species categories. The aim was to discover whether the edge view of the specimens incorporated meaningful information about the differences between species after eigenshape analysis.

Thus the MORTEST analysis is not a method for identifying the species of the *Morozovella* lineage of the Palaeocene, but rather is an investigation of the importance of the edge view in contributing to the diagnostic ability of a micropalaeontologist engaged in identifying these species.

The species and sample levels investigated in the MORTEST study are detailed in Table 2. All but one of these samples were of morozovellids orientated in edge view. One sample however, referred to as MORTESTUMB, was analysed in umbilical view to serve as a comparison with an edge view sample from the same horizon.

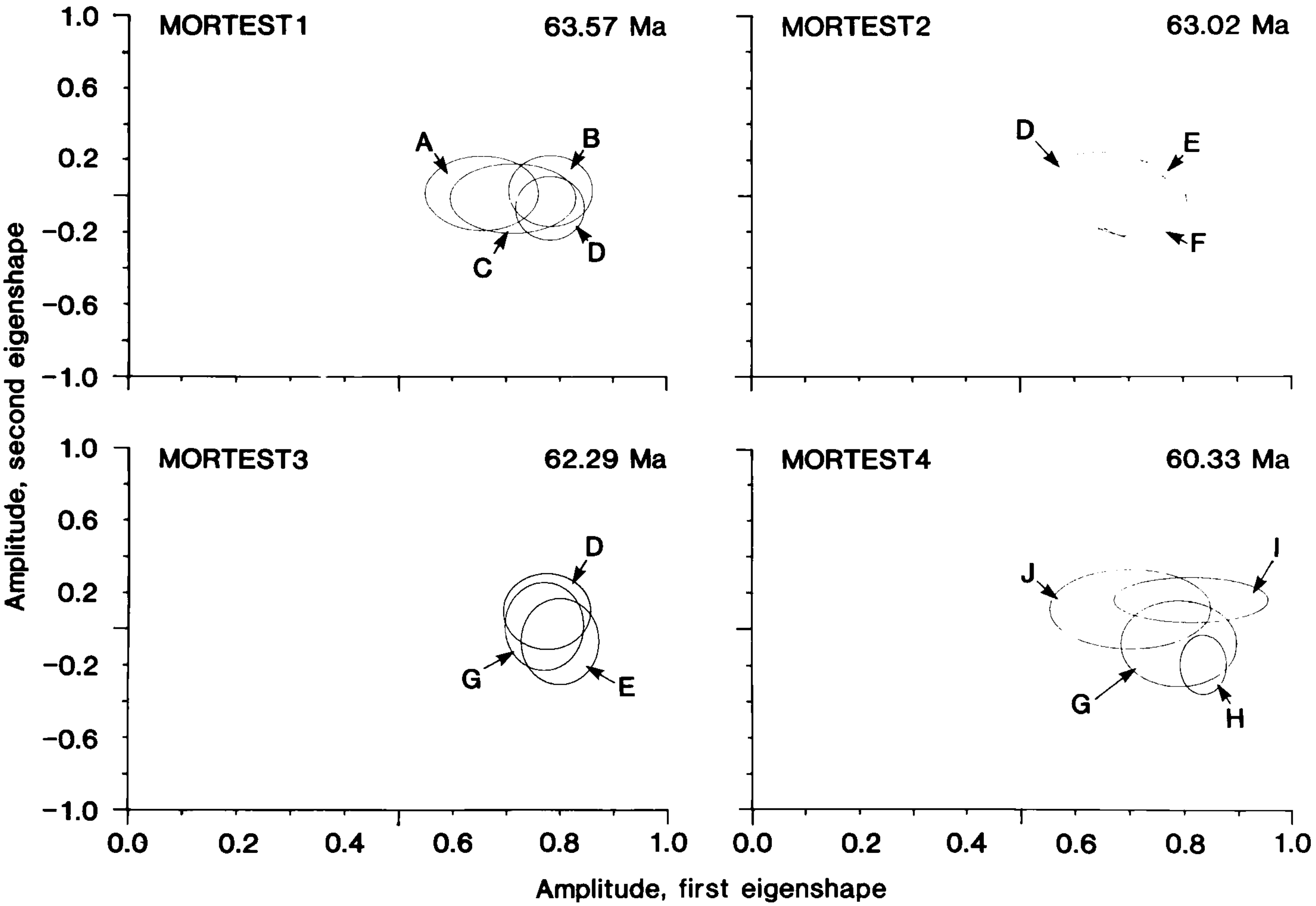

Fig. 2. Results of the MORTEST analysis. A = *M. trinidadensis* B = *M. praecursoria* C = *M. uncinata* D = *M. conicotruncata* E = *M. praeangulata* F = *M. angulata* G = *M. angulata* forma *protocarina* H = *M velascoensis* I = *M. occlusa* J = *M. edgari.*

RESULTS OF THE MORTEST ANALYSIS

Fig. 2 illustrates the correlation of the specimens that comprise each species group with the 1st and the 2nd eigenshapes for all MORTEST sample levels. The area covered by the ellipse, which represents each species, is one standard deviation of the mean eigenshape calculated for each species on both the 1st and 2nd eigenshape axes, hence the ellipse shows the range of variation associated with the species in the two axes of greatest variability (the 1st and 2nd eigenshapes).

MORTEST1 illustrates that in edge orientation the cluster of ellipses that represent the species *M. trinidadensis*, *M. praecursoria*, *M. uncinata* and *M. conicotruncata* are very close together indicating that the edge view outline of these species is not very different. It is, however, interesting to note that the relatively 'advanced' morozovellid *M. conicotruncata* is the species that shows the greatest difference from the most 'primitive' morozovellid *M. trinidadensis* and is also the species that shows the smallest area on the graph and is therefore the most consistently recognisable with respect to its edge view.

MORTESTUMB (Fig. 3) also illustrates that the greatest separation between the species areas is between *M. trinidadensis* and *M. conicotruncata*. However in this case, the area of the ellipse for the species *conicotruncata* is much greater in the umbilical orientation than in the edge orientation. A feature of interest in both MORTEST1 and MORTESTUMB is the great area of edge and umbilical variability illustrated by *Morozovella uncinata*; it is apparent that this species cannot be separated from other early morozovellids on the basis of its outline.

MORTEST2 illustrates that the species *M. conicotruncata*, *M. praeangulata*, and *M. angulata* have virtually identical edge views. The overlap between *M. praeangulata* and *M. angulata* is almost complete, but the centres of the ellipses for these two species are slightly offset from the centre of the ellipse for *M. conicotruncata*.

Table 2. Sample levels with component species for MORTEST analyses.

	Sample	Depth (mbsf)	Age (Ma)
MORTEST 1	11/5/120*	102.1	63.57
MORTESTUMB	11/5/120*	102.1	63.57
MORTEST 2	11/5/ 0*	100.9	63.02
MORTEST 3	11/2/ 90*	97.3	62.29
MORTEST 4	10/6/ 30	93.2	60.32

A = *M. trinidadensis*
B = *M. praecursoria*
C = *M. uncinata*
D = *M. conicotruncata*
E = *M. praeangulata*
F = *M. angulata*
G = *M. angulata* forma *protocarina*
H = *M. velascoensis*
I = *M. occlusa*
J = *M. edgari*

MORTEST3 confirms that the intermediate morozovellids (e.g. *M. praeangulata*, *M. angulata*, *M. conicotruncata* and *M. angulata* forma *protocarina*) do not show significant differences between their edge outlines.

However, the late stage morozovellids depicted in MORTEST4 show that the species *M. velascoensis*, *M. edgari*, and *M. occlusa*, are quite distinctly separated from each other with regard to the eigenshape analysis of their edge views. *M. occlusa* and *M. edgari* do show some degree of overlap with each other but are separated from *M. velascoensis*. All three of these late stage morozovellids overlap with the ellipse describing the edge view variability of *M. angulata* forma *protocarina*.

DISCUSSION OF THE MORTEST ANALYSIS

These results indicate that most Palaeocene morozovellid species are not recognisable on the basis of their edge view alone. Thus *M. uncinata* encompasses a wide range of variability in both edge and umbilical views (MORTEST and MORTESTUMB in Fig. 3) and overlaps with *M. trinidadensis* and *M. praecursoria*. This is significant because of the long standing controversy concerning the systematics of the Early Palaeocene morozovellids. Berggren (1965) considered that the species *praecursoria* was a senior synonym of *trinidadensis*, whereas Blow (1979) considered *inconstans* a senior synonym of *trinidadensis*. Blow (1979) also considered that *praecursoria* was a senior synonym of *uncinata* and abolished the latter species accordingly. More recently, Toumarkine & Luterbacher (1985) have recognised all these species in their comprehensive review of the low latitude Palaeogene planktonic foraminifera.

The data from the eigenshape analysis presented here supports the view that this plexus of species is very similar.

The differentiation of the early morozovellids is complex and relies on the assessment of characters of degree rather than of kind: thus *M. uncinata* has fewer chambers in the final whorl than *M. praecursoria* but the same number of chambers as *M. trinidadensis*. *M. uncinata* and *M. trinidadensis* are therefore distinguished by the number of chambers in the final whorl that bear muricae. In *M. trinidadensis* this is typically only the initial two chambers of the final whorl whereas in *M. uncinata* the initial three or more (but never the final chamber) chambers of the final whorl are muricate.

During the shape capture, it was observed that the muricate nature of the morozovellid test was often captured by the data acquisition system. The fact that the variable nature of the distribution of muricae on the early chambers of the final whorl of the primitive morozovellids does not contribute to the species discriminating ability of the eigenshape analysis must therefore be accounted for. A possible explanation of this is that the muricae on the early chambers of the final whorl of these primitive morozovellids were not sufficiently developed to contribute to the Zahn & Roskies shape function or, alternatively, that the variability of the degree of murical covering of the test was not sufficiently pronounced to contribute to the lower order eigenshapes. It is possible however, that muricae contribute to higher order eigenshapes.

Another important feature of the MORTEST analysis of the primitive morozovellids is that although all the individual species overlap their ranges of variability, *M. conicotruncata* (an intermediate morozovellid) is the least similar to the morozovellid progenitor *M. trinidadensis* (MORTEST1). This indicates that the progessive development of the morozovellid lineage away from the essentially globigeriniid morphology of *S. pseudobulloides* to the angulo-conical morphology of *M. velascoensis* is measurable in the edge view orientation of the specimens of this lineage. Also of note is the discrete range of *M. conicotruncata* in MORTEST1 and MORTEST2 (Fig. 2). The range of variability of the species is narrow in the edge view orientation, which indicates that this feature is a useful diagnostic criterion in the discrimination of this species.

The plot for MORTESTUMB (Fig. 3) confirms the conclusions drawn from MORTEST1. The range of variability for *M. uncinata* is again large relative to other species from the same horizon. *M. trinidadensis* and *M. conicotruncata* again lie at opposite ends of the spectrum of variability on the 1st eigenshape. An interesting difference between MORTEST and MORTESTUMB is the rather large range of variability shown by *M. conicotruncata* in the umbilical orientation. This contrasts with the discrete range shown by this species in the edge view. It may be attributed to ontogenetic variation, a feature that is apparently less obvious in the edge view orientation.

MORTEST2 illustrates that there is virtually no difference in the edge views of the species *M. conicotruncata*, *M. praeangulata* and *M. angulata*. The same is true for MORTEST3 where there is no separation of the species *M. angulata* forma *protocarina*, *M. praeangulata* and *M. conicotruncata*.

MORTEST4, however, shows several features of interest. The most noticeable of these is the small variability of *M. velascoensis*. This indicates that the shape of this species is well defined in the edge view although it does overlap the range of variability of *M. angulata* forma *protocarina*. The species *M. edgari*, *M. occlusa* and *M. angulata* forma *protocarina* have greater ranges of variability.

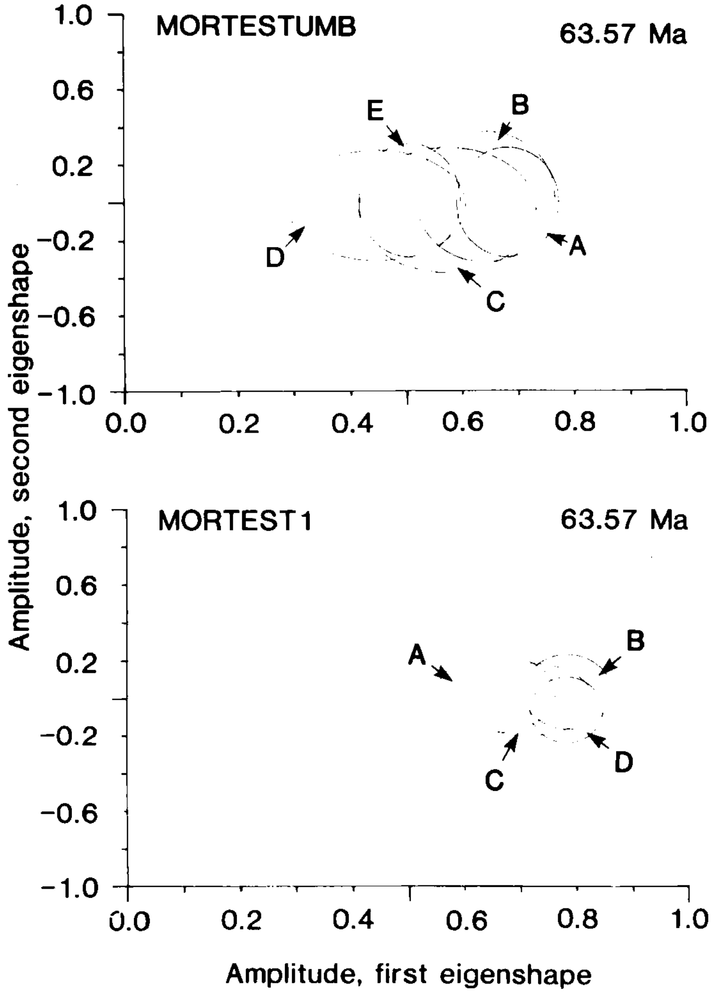

Fig. 3. Results of MORTESTUMB together with MORTEST1. Key as for Fig. 2.

In this paper we interpret *M. edgari* and *M. occlusa* as close relatives to *M. velascoensis* and suggest that the common ancestor of all three species is *M. angulata* forma *protocarina*. This morphotype is therefore characterised by a morphology intermediate between *M. angulata* and *M. velascoensis*. The separation of *M. velascoensis*, *M. occlusa* and *M. edgari* in MORTEST4 is therefore interpreted as indicating a divergence of *M. velascoensis* from *M. occlusa*/*M. edgari* during their evolution from the common ancestor *M. angulata* forma *protocarina*.

The overlap of *M. occlusa* and *M. edgari* indicates a strong similarity in the shape of their edge views. All three of these late stage morozovellids (*M. velascoensis*, *M. occlusa* and *M. edgari*) overlap with the variability spectrum of *M. angulata* forma *protocarina*, a feature consistent with their relationship to this hypothesised ancestor.

The greater spread of all four of the species in MORTEST4 illustrates the relatively great difference in the edge views of these species compared to the MORTEST analyses from older horizons.

THE STRUCTURAL EVOLUTION OF THE PALAEOCENE *MOROZOVELLA* LINEAGE

In an important paper Malmgren *et al.* (1983) applied eigenshape analysis to a study of the phylogenetic evolution of the *Globorotalia plesiotumida*/*G. tumida* transition across the Miocene/Pliocene boundary. The morphological development of *Morozovella velascoensis* from *Subbotina pseudobulloides* offers a similar test of the eigenshape method on an ancient lineage.

There are points of difference between the present study and that of Malmgren *et al.* (1983). The most important of these is that the evolution of the morozovellids involves patterns of speciation superimposed on the phylogenetic shape change of the lineage. Thus it is a more complex analysis than that of the *plesiotumida*/*tumida* transition. This is illustrated by Fig. 1 where can be seen the overlapping ranges of forms such as *M. angulata* and *M. angulata* forma *protocarina*. This is significant because the investigations of this author and others (e.g. Berggren, 1968; Toumarkine & Luterbacher, 1985) indicate that *M. angulata* is the direct phyletic ancestor of *M. velascoensis*. Because of this feature, the samples for the analyses were composed of a mixture of both ancestor and descendant species where both occurred in sufficient numbers. This had the effect of providing an average morozovellid shape at each sampled horizon. In a future study, it would be instructive to measure shape variations in each of the component species of the morozovellid lineage to provide a more comprehensive picture of the pattern of phylogenetic evolution in this group. It would also be advantageous to extend such a study closer to the Cretaceous/Tertiary boundary in order to incorporate data from the beginnings of the genus *Morozovella*. In addition, it would be useful to investigate the pattern of structural evolution in the *Morozovella* lineage from another site for comparative purposes.

Before considering the data, it is worth emphasising that in both this study and that of Malmgren *et al.* (1983), the protocol of the investigation was directed by *a priori* knowledge of the sequence of species in the investigated lineages. The recognition of biological homology, upon which studies such as this are based, can only be done using the knowledge and skill of the micropalaeontologist, and this skill will always remain as the basis for studies of evolution in the fossil record.

Fig. 4 illustrates the amplitude of the 2nd eigenshape for all the samples analysed. It is necessary, when using the eigenshape technique to measure evolutionary shape change, to perform two separate analyses. The

Table 3. Age, size (area) and amplitude of second eigenshape for MOROZALL samples.

No.	Age, (Ma)	Area (sq. mm)	95% conf. (±)	Amplitude (radians)	95% conf. (±)
1)	56.77	0.0373	0.00423	0.244	0.110
2)	57.82	0.0484	0.00696	−0.210	0.159
3)	58.06	0.0525	0.00584	−0.531	0.101
4)	58.42	0.0379	0.00376	−0.229	0.123
5)	58.65	0.0469	0.00640	0.302	0.123
6)	58.89	0.0605	0.00692	−0.426	0.116
7)	59.06	0.0382	0.00511	−0.116	0.121
8)	59.22	0.0524	0.00664	0.601	0.109
9)	59.34	0.0451	0.00601	−0.592	0.160
10)	59.44	0.0472	0.00512	0.284	0.122
11)	59.55	0.0342	0.00354	−0.480	0.163
12)	59.66	0.0411	0.00282	0.309	0.168
13)	59.77	0.0415	0.00435	0.428	0.157
14)	59.88	0.0479	0.00599	0.644	0.131
15)	60.08	0.0443	0.00514	0.174	0.164
16)	60.20	0.0503	0.00776	−0.153	0.150
17)	60.32	0.0494	0.00787	0.219	0.138
18)	60.50	0.0545	0.00495	−0.235	0.167
19)	60.52	0.0572	0.00618	0.505	0.106
20)	60.22	0.0538	0.00601	−0.593	0.166
21)	60.32	0.0623	0.00833	−0.285	0.109
22)	61.86	0.0519	0.00766	0.289	0.135
23)	61.68	0.0420	0.00298	−0.363	0.157
24)	61.98	0.0473	0.00722	−0.379	0.131
25)	62.10	0.0455	0.00533	−0.484	0.161
26)	62.29	0.0478	0.00458	−0.333	0.147
27)	62.53	0.0367	0.00325	−0.171	0.126
28)	62.71	0.0426	0.00285	0.073	0.138
29)	62.83	0.0347	0.00336	−0.101	0.103
30)	63.02	0.0373	0.00326	−0.029	0.150
31)	63.14	0.0387	0.00488	0.240	0.110
32)	63.30	0.0352	0.00338	0.357	0.128
33)	63.46	0.0366	0.00276	−0.245	0.136
34)	63.57	0.0328	0.00194	0.119	0.127
35)	63.63	0.0298	0.00183	0.278	0.124
36)	63.69	0.0310	0.00161	0.122	0.110
37)	63.75	0.0260	0.00187	0.376	0.162
38)	63.82	0.0283	0.00157	0.631	0.147
39)	63.88	0.0254	0.00165	0.085	0.109
40)	63.95	0.0254	0.00128	0.034	0.107
41)	64.00	0.0282	0.00150	−0.031	0.108

first of these (entitled MOROZ in our experimental protocol) is the eigenshape analysis of each individual sample. This provides the mean shapes (the eigenshapes) that represent the shape of the specimens in the sample. The second analysis (MOROZALL) is the eigenshape analysis of all the MOROZ analyses which yields the eigenshapes which can represent the entire lineage. As discussed earlier in this study, we follow previous usage (Lohmann & Malmgren, 1983; Malmgren *et al.*, 1983) and use the amplitude of the second eigenshape to portray the shape change occurring in this lineage (Table 3).

Fig. 4 also shows the rate of turnover of species in the Palaeocene members of the genus *Morozovella* during the interval considered in this study (Table 4). Turnover in this study refers to the rate of origination per million years plus the rate of extinction per million years of the Palaeocene members of the genus *Morozovella*. This information is based on the analysis of Corfield (1987a).

Table 4. Taxonomic turnover (Number of species originations + species extinctions per million years) in the Palaeocene *Morozovella* lineage (from Corfield, 1987a).

Age (Ma)	Turnover (originations + extinctions/My)
61	0
62	6
63	9
64	3
65	0

Because this study of structural evolution was confined to samples taken from DSDP 577, there is a hiatus between 60.5 Ma and 61.6 Ma (Corfield, unpub. PhD thesis; Corfield & Shackleton, in prep. b) which accounts for the gap between the MOROZ samples near these levels in Figs. 4 and 5. This hiatus affects only the final morozovellid transformation from *M. angulata* forma *protocarina* to *M. velascoensis* and does not invalidate the earlier stages of the structural evolution of *Morozovella*.

In horizons older than the hiatus, there is a trend towards decreasing amplitude values, marked A on Fig. 4. The samples above the hiatus do not show a systematic trend in the amplitude of the second eigenshape. Thus, after the evolution of *M. velascoensis*, shape fluctuations are not directional. However, the amplitude change in the *Morozovella* lineage marked A on Fig. 4 can be seen to be contemporaneous with the peak in species turnover of the Palaeocene morozovellids.

SIZE CHANGE IN THE PALAEOCENE *MOROZOVELLA* LINEAGE

It is well known that the basal Danian is characterised by very small planktonic foraminifera with a relatively simple globigeriniid morphology (Blow, 1979; Toumarkine & Luterbacher, 1985; Hsu, 1986). This Danian fauna is replaced at 63.0 Ma by the diversifying morozovellids (Corfield, 1987a). Fig. 5 illustrates the size change in the *Morozovella* lineage (Table 3). It is apparent that a feature of the structural evolution of the Palaeocene morozovellids is a marked increase in size from the oldest sample (64.0 Ma) to the sample just below the hiatus (61.6 Ma); this trend is illustrated as line B on Fig. 5.

This increase in size is contemporaneous with the peak in morozovellid turnover and the structural transition from *S. pseudobulloides* to *M. angulata*

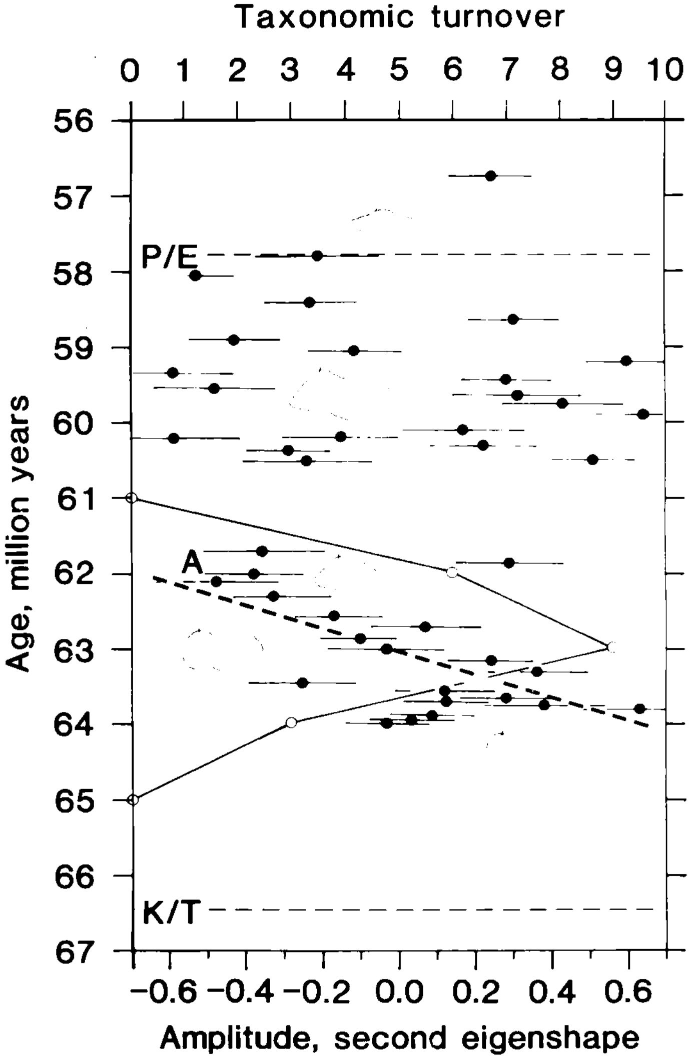

Fig. 4. Amplitude of second eigenshape plotted against age and taxonomic evolution in the Palaeocene *Morozovella* lineage. A = regression line illustrating the structural transition referred to in the text. Slope = 1.51, r = .58 (p = 0.01). Taxonomic turnover = species originations + species extinctions per million years in the Palaeocene *Morozovella* lineage.

forma *protocarina*/*M. velascoensis* illustrated in Fig. 4. Subsequently, there is a trend toward decreasing size (line C on Fig. 5). Younger samples (all composed of *M. velascoensis*) show no systematic changes in size.

SPECIES SELECTION IN THE PALAEOCENE *MOROZOVELLA* LINEAGE

Comparison of Figs. 4 and 5 illustrates that as the shape change occurred from the morozovellid progenitor *S. pseudobulloides* to *M. velascoensis*, there was a contemporaneous increase in the mean size of the members of the lineage. This trend can be compared with the dataset of Malmgren *et al.* (1983) which demonstrated that the phylogenetic transition from *G. plesiotumida* to *G. tumida* was accompanied by an increase in the size of the test. In fact, comparison of figs. 4 and 5 in the paper by Malmgren *et al.* (1983) shows a rather close covariance between size and the amplitude of the second eigenshape throughout the sequence. Our data do not show such covariance although it is apparent from a comparison of line A on Fig. 4 and line B on Fig. 5 that there is a negative relation between the size and shape change in the older part of this lineage. It should, however, be emphasised that the eigenshape technique removes the influence of size on shape change data. Thus, this apparent correlation is not an artefact of the statistical techniques employed.

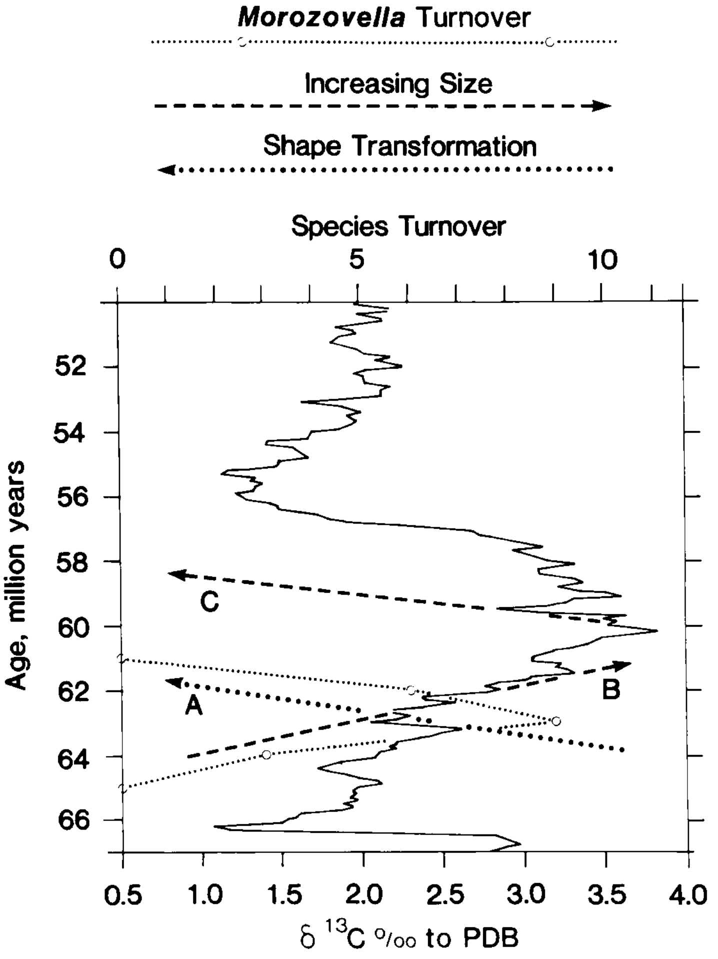

Fig. 5. Size change in the Palaeocene *Morozovella* lineage plotted against age and taxonomic turnover. B = regression line for all samples below hiatus illustrating size increase in this lineage. Slope = −87.28, r = −0.91 (p = 0.001). C = regression line illustrating size change in younger horizons. Slope = 48.99, r = .38 (p = 0.1).

It is worth noting that this event is the first such large scale burst of evolutionary activity within the Cenozoic planktonic foraminifera. The locus of this activity is at 63 Ma, 3.6 million years *after* the Cretaceous/Tertiary boundary. This suggests that the K/T event was not followed immediately by an explosive burst of evolution (Hsu, 1986; Gerstel *et al.*. 1986) as the planktonic foraminifera re-radiated into the 'strangelove' ocean. Rather, it appears that the undifferentiated *G. eugubina* fauna, characteristic of the earliest Palaeocene, persisted with low levels of species turnover and diversity (Corfield & Shackleton, in prep. a) until the evolution of the Palaeocene morozovellids.

The close parallel between the trend toward increasing size and the directional shape change in the *Morozovella* lineage illustrated in Figs. 4 and 5 is also related to the taxonomic turnover that occurs in the Palaeocene members of this genus.

Thus, the speciation events that produced the members of this genus were accompanied by the structural evolution of the typical morozovellid characters; the muricate angulo-conical test with the muricocarina. This pattern of directional shape change superimposed on speciation we interpret as an example of species selection (Stanley, 1975; Gould & Eldredge, 1977).

The lack of directional shape change after the evolution of *M. velascoensis* is comparable with the non-directional fluctuations in the shape of members of the *G. plesiotumida*/*G. tumida* lineage in the Late Miocene and Plio-Pleistocene Indian Ocean described by Malmgren *et al.*, 1983. They interpret this as random oscillations about a stationary morphotype. A similar situation appears to prevail after *M. velascoensis* evolves.

It is now well known that the members of the genus *Morozovella* rank as surface water dwelling species on the basis of their oxygen and carbon isotope composition (Boersma *et al.*, 1979; Shackleton *et al.*, 1985). It has also been suggested that the Palaeocene period was characterised by increased productivity in the surface waters of the ocean (Shackleton, 1987) and that this had a major effect on the patterns of taxonomic evolution in the planktonic foraminiferal faunas of the Palaeocene and Early Eocene (Corfield, 1987a).

The increase in surface water productivity during the

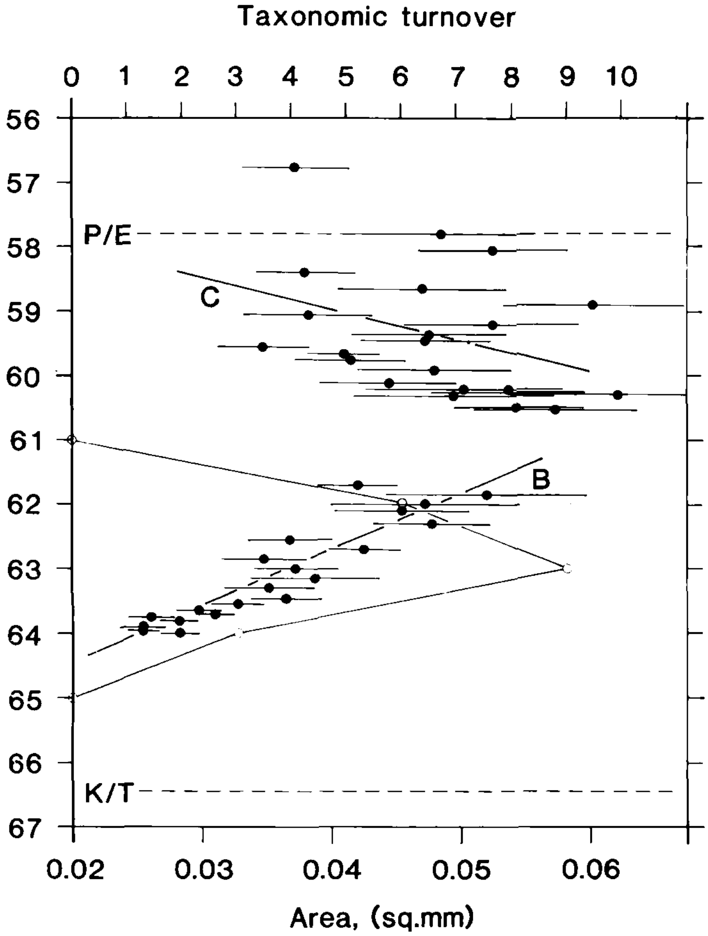

Fig. 6. Species selection in the Palaeocene members of the genus *Morozovella* plotted against the δ^{13}C curve for the same interval. Open circles connected by the small dotted line indicate the rate of species turnover (number of originations + extinctions per million years) within the Palaeocene morozovellids.

Palaeocene implies an intensification of the selective pressures operating upon the surface dwelling planktonic foraminifera of this interval. We suggest that this may have been the cause of the increase in species turnover and the directional shape and size change within the morozovellids in these horizons. These events together comprise an example of species selection.

To qualify as species selection, two conditions must be satisfied (Gould & Eldredge, 1977), (1) that it is the species, rather than the individual that is the unit of selection (Wright's Rule), and (2) that evolution proceeds rapidly.

In the example discussed here, it is clear that relatively large units (morozovellid species) are being selected for, thereby resulting in the progressive development of the typical morozovellid morphology exhibited by *M. velascoensis*. It is this selection for a particular shape that results in the directional change in the second eigenshape marked A on Fig. 4. The relatively short duration of speciation events compared with subsequent species' ranges indicates that the evolution of the Palaeocene morozovellids is an example of punctuated equilibrium (Eldredge & Gould, 1972; Gould & Eldredge, 1977). Therefore, since both criteria are satisfied in this example, we believe that the evolution of the Palaeocene morozovellids provides a good example of species selection. Fig. 6 illustrates the relationship between shape and size change and speciation (species selection), in the context of the increase in ocean productivity, and therefore the intensification of selective pressures in the surface waters of the ocean, during the Palaeocene and Early Eocene.

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