Morphometric Analysis of Selected Benthic Foraminifera from Cape Roberts Project (CRP) and CIROS-1 Cores, Victoria Land Basin, Antarctica

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Abstract - Size measurements and morphological analyses of *Globorotalia umbilicata* (Brady) and *Stomatocyclophora* cf. *schreiberiana* (Czjzek) from CRP and CIROS-1 cores have revealed discrete morphological adaptations of these species through time, which occur mainly in terms of size changes. Test size and morphological changes exhibited by the studied species are probably related to a complex interaction of several environmental parameters including dissolution, CaCO3 availability, trophic conditions, salinity, water depth, dissolved oxygen content and temperature. Bottom water temperature and trophic conditions emerge as the most important factors in controlling the observed variations. Besides this, the morphometric analysis allowed us to discriminate between different populations of the same species at different stratigraphical levels, which demonstrates the potential of this method as a tool for regional biostratigraphical correlations.

INTRODUCTION

Foraminiferal distribution in mid-Cenozoic strata from the CIROS-1 drillhole, 70 km southeast of the CRP drillholes off the southern Victoria Land coast (Fig. 1, CRST, 2000), has shown that assemblages with cosmopolitan taxa were replaced by faunas characterised by a distinct <i>polar</i> affinity during the latest Eocene (Webb, 1989; Coccioni & Galeotti, 1997). This faunal turnover, which marks the local disappearance of several species of *Cibicidoides* and *Anomalinaeoides* and of some agglutinating forms in the benthic foraminiferal assemblages, may be interpreted as reflecting climatic deterioration during the Eocene-Oligocene transition (see Prothero, 1994, for a review). Oligocene-Miocene Ross Sea foraminiferal assemblages are characterised by very little taxonomic turnover (Galeotti and Coccioni, 1998; Strong and Webb, 1998, 2000; Galeotti et al., 2000; Cape Roberts Science Team, 2000; Strong & Webb, this volume). Together with the virtual absence of planktic species, the presence of taxonomically homogeneous benthic foraminiferal assemblages in the Cenozoic Ross Sea hampers a detailed biostratigraphical and palaeoenvironmental reconstruction of the area.

To overcome this problem, we explore the possibility that morphometric changes of selected benthic foraminiferal species from CRP and CIROS-1 cores might serve as a biostratigraphical and palaeoenvironmental tool. Variations of morphological parameters have, in fact, two potential applications:
- data from species in which morphological changes are environmentally controlled can be used as proxies for sea-floor palaeoenvironmental conditions, by relationships known in modern oceans;
- inheritable morphological adaptation patterns may be useful in establishing phylogenetic relationships among species and represents, therefore, a useful biostratigraphical tool.

This study represents a first attempt to ascertain if selected species of benthic foraminiferal exhibit test-size and morphological changes through time in the Ross Sea Cenozoic, and to relate these to environmental parameters.

MATERIAL AND METHODS

Morphometric analysis was performed on a total of 212 samples including 40 new samples from the CRP-2/2A and CRP-3 cores and on samples already studied from the CIROS-1 core (109 sample by Coccioni & Galeotti, 1997), CRP-2/2A core (39 samples by Galeotti et al., 2000), and CRP-1 core (24 samples by Galeotti & Coccioni, 1998). Analysed samples come from the following stratigraphical intervals:
- CIROS-1: 702-366 meters below the sea floor (mbsf), spanning the upper Eocene-lowermost Oligocene according to Wilson et al. (1998);
- CRP-3 core: 338-16 mbsf, spanning the lower Oligocene according to Cape Roberts Science Team (2000);

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- CRP-2/2A core: 57-624 mbsf, spanning the lower Oligocene-middle Miocene according to Wilson et al. (2000);
- CRP-1 core: 55-147 mbsf, spanning the lower Miocene according to Roberts et al. (1998).

The stratigraphic intervals studied can, therefore, be considered as parts of a composite sequence spanning the upper Eocene lower sequence of the CIROS-1 core to the lower Miocene CRP-1 core (Fig. 1).

A total of 48 samples, 38 from CIROS-1, 7 from CRP-3, 2 from CRP-2/2A, and 1 from CRP-1 proved to contain one or more of the species selected for this investigation.

Morphometric parameters measured on *Globocassidulina subglobosa* and *Stainforthia cf. schreibersiana* are depicted in figure 2 and are defined below:

*Globocassidulina subglobosa* (Brady) (= *Cassidiilina subglobosa* Brady, 1884):
- d: minimum umbilical view diameter
- D/d ratio where D and d are the maximum and the minimum umbilical view diameter, respectively;

*Stainforthia cf. schreibersiana* (Czjzek) (= *Virgulina schreibersiana* Czjzek, 1848):
- Length of the test
- Width of the test
- Side view angle

Images of single specimens were captured with a videocamera attached to a stereomicroscope, and transferred to a 23 inch, high resolution, flat monitor. Repeated measurements of the same specimens on video images, show an error less than 0.5 %, therefore demonstrating the high precision of the method.

All the samples containing any of the selected species were used in this study, including those containing a single specimen. This approach clearly affects the statistical value of the analysis when evaluating high-frequency trends. Still, it allows evaluation of broader trends in the composite sequence since, independently from the low number of specimens measured in each single sample, average values may be considered to be representative of specific intervals, when a large enough number of specimens is taken into account. To test this assumption the measured variables have been plotted separately for groups of cases defined by assemblages labelled as A-D in figure 1, and the mean and standard error values for these assemblages presented in box plot figures.

**RESULTS**

The morphometric results from this study are presented graphically below in figures 3 to 8. The measurements made on each sample can be obtained by contacting the first author.

No data on *G. subglobosa* and *S. schreibersiana* have been obtained from the CRP-1 core. The former taxon occurs in a single sample with only four specimens, and specimens of what might be the latter show morphological dissimilarity from *S. cf. schreibersiana* that may justify separation into a different species.
Variations of intraspecific morphometric parameters for *G. subglobosa* and *S. cf. schreibersiana* in the lower sequence of the CIROS-1 core, that is from the bottom to 366 metres below the sea floor (mbsf), are shown in Figures 3 and 6, respectively. Figures 4 and 7 show a comparison of values obtained for the two species from CIROS-1 and CRP cores. The central tendency and variation statistics for *G. subglobosa* and *S. cf. schreibersiana* within assemblages A to D are illustrated in Figures 5 and 8, respectively.

*Globocassidulina subglobosa* (Brady):

As already reported by Webb (1989) and Coccioni and Galeotti (1997) the range of this species in the CIROS-1 core is limited to the lower sequence, that is, from the lowermost core to the major hiatus recorded at 366 mbsf. In particular, this species occurs more consistently within two intervals between ca. 680 mbsf and 635, and between ca. 470 and ca. 410 mbsf, corresponding to assemblages A and B, respectively. These two intervals are characterised by rather different *G. subglobosa* populations in terms of test size and D/d ratio (Figs. 4, 5). Assemblage A (lowermost part of CIROS-1 core) shows a high variability of test size (d ranging from 112 to 392 μm) whereas populations from the 470-410 mbsf interval (i.e. assemblage B) show a restricted variability and lower average values of test size (d ranging from 138 to 299 μm). Accordingly, calculation of the confidence intervals on *G. subglobosa* suggests that the two populations are significantly different in terms of test size and D/d ratio (Fig. 5).

A higher average value of the D/d ratio, which results in the development of a more elongate morphology and a tendency to uncoil, characterises the record of *G. subglobosa* from the upper interval. However, the average value of this parameter in assemblage C from CRP-3 core is similar to that observed in assemblage A from the lowermost part of CIROS-1 Core (Figs. 4 and 5).

Specimens of *G. subglobosa* from CRP-3 core material show a wide range of test size («d» ranging from 186 μm to 456 μm). However, the lower part of the surveyed interval at CRP-3 is characterised by a size range similar to that observed in the upper part of the surveyed interval of CIROS-1. Larger specimens are confined to the upper part of CRP-3 down to a depth of 114.34 mbsf.

Uniformly small-sized specimens of *G. subglobosa* occur in the lower part of the CRP-2/2A core («d» ranging from 127 μm to 177 μm). Although based on only 21 specimens recovered from 2 samples (580.90 mbsf and 582.5 mbsf) these data can be compared to samples of the same dimension (ca. 10 specimens) showing significantly larger test size variation from both CRP-3 and CIROS-1 cores. Moreover, the standard error-based box and whisker plot (Fig. 5) allows us to clearly separate this population, corresponding to assemblage D, from assemblage A-C, in terms of test size.

*Stainforthia cf. schreibersiana* (Czjzek):

Similarly to *G. subglobosa*, the range of *S. cf. schreibersiana* in CIROS-1 is limited to the lower part of the core, that is, from the lowermost core to the hiatus recorded at 366 mbsf (Webb, 1989; Coccioni & Galeotti, 1997). Specimens from the lower part of the surveyed interval in CIROS-1 core,
corresponding to Assemblage A, are never longer than 500 μm (Fig. 6). The maximum length value (672 μm) is recorded in the upper part of the studied interval in the CIROS-1 core. Assemblage B, from the upper part of the studied interval of CIROS-1 core, exhibit higher length average values (Fig. 6). Specimens of S. cf. schreiberiana exhibit a tendency to become larger and more elongate from older to younger intervals in CIROS-1.

Larger test size average values are observed also in the CRP-3 core material where S. cf. schreiberiana specimens have length values between 373 μm and 648 μm and width values between 123 μm and 224 μm (Fig. 7). Specimens from CRP-3 are on average larger and more elongate than those observed in the CIROS-1 core (Figs. 7 and 8). In the CRP-2/2A core material, S. cf. schreiberiana shows a very broad range of length and width values, and side view angle average values are similar to those observed in CIROS-1 core.

DISCUSSION

As previously mentioned, the small number of specimens occurring in several samples does not allow a statistically thorough evaluation of high-frequency changes in the studied species. However, broader trends can be observed when comparing populations from different stratigraphical intervals (Figs. 6 & 8).

PALAEOECOLOGY

Intraspecific morphometric changes through time derive from adaptation to ecological factors and/or evolutionary trends. It is difficult to separate intraspecific morphological variations induced by one or the other mechanism. Moreover, intraspecific evolutionary changes may also result from adaptation
to environmental conditions. However, a suitable method by which we might recognise trends related to evolution is the identification of irreversible trends, which are most likely related to evolutionary processes. On the other hand, temporary adaptations to environmental parameters are likely to result in reversible changes. Morphometric changes observed in *G. subglobosa* and *S. cf. schreiberiana*, appears to be repetitive and are better explained in terms of a response to palaeoenvironmental fluctuations.

Many organisms show a good correlation between test shape and the environment in which they live. To a certain degree, this applies also to benthic foraminifera, which have been shown to develop morphological adaptations dependent on several environmental parameters, including food availability, oxygenation, temperature and salinity (Murray, 1991). The subdivision into morphotypic groups of both calcareous (Corliss, 1985; Bernhard, 1986; Corliss and Chen, 1988) and agglutinating (Jones and Charnock, 1985) benthic foraminiferal assemblages has been widely applied in recent years for palaeoenvironmental reconstructions in Mesozoic and Cenozoic sequences (Koutskos & Hart, 1990; Kaitho, 1991; Coccioni & Galeotti, 1994; Nagy et al., 1995).

The detection of intraspecific morphological changes through time, on the other hand, offers the possibility of deciphering the environmental factors controlling the distribution of ecophenotypes. Morphological variations of benthic foraminiferal tests in response to changes in ecological parameters are summarised and briefly discussed by Boltovskoy et al. (1991). As evidenced by the latter authors, intraspecific morphological changes seem to affect mainly the size and the ornamentation of the test although other morphological features have been only occasionally discussed. Water depth, salinity, temperature, dissolved oxygen concentration and food availability are the principal limiting factors to benthic foraminifer distribution (see Murray, 1991) and also affect the relative proportion of different ecophenotypes (Boltovskoy et al., 1991).

Several environmental processes might account for the observed variability of the three analysed species which are mainly seen in terms of size changes through time from the upper Eocene lowermost sequence in CIROS-1 core to the lower Miocene CRP-3 core. In Recent benthic foraminiferal species, size variations may result from phenotypic variation due to the influence of environmental variables such as temperature (Lewis and Jenkins, 1969; Theyer, 1971), salinity and dissolved oxygen content (Lutze, 1964; Theyer, 1971). Deciphering the factor(s) leading to decreasing test size in *G. subglobosa* and concomitant increasing test size in *S. cf. schreiberiana* is further complicated by the fact that the test size variations observed in these species may result from different ecological parameters. Moreover, it is also possible that the two species reacted in opposite ways to the same ecological variations. For example, some species including *Chiostomella aolina*, *Chiostomella ovoidea*, *Cyclammina*...
cancellata, Haplophragmoides bradyi, Hoeglundina elegans, Laticarina pauperata, Pyrgo murrhina, Pyrgo rigens, Pyrgoella sphæra, Robulus thalmanni, and Sphaeroidina bulboides all respond to increasing water depth by increasing their test size (Pflum and Frerichs, 1976; Bandy, 1963; Theyer, 1971). However, some others including Hyalinea balthica, Lagenonodosaria scalaris, Glandulina laevigata, G. subglobosa, and Eggerella advena, have been shown to respond in the opposite way (Resig, 1963; Colom, 1970; Corliss, 1979). As stated by Boltovskoy et al. (1991), it is difficult to separate the influence of different interrelated ecological parameters from these studies although it is clear that the above mentioned adaptations might be controlled by factors changing with bathymetry, in particular, CaCO₃ dissolution and temperature.

For ease of discussion, we separate each individual factor, although it is clear that a combination of two or more of them might account for the observed morphometric trends.

**DISSOLUTION**

In a study of size variations in *G. subglobosa* from a bathymetric transect in the southeast Indian Ocean, Corliss (1979) observed the existence of two distinct size groups in this deep-water species. According to Corliss (1979), the first group, characterised by uniformly small tests, occurs at water depths greater than 3,500 m whereas a second group showing high variability and large mean length value is found at depths generally less than 3,500 m. A
correlation analysis between size data and nine independent variables including salinity, dissolved oxygen content, and temperature, showed that a significant inverse correlation exists between the size of *G. subglobosa* and CaCO₃ dissolution.

Following Corliss (1979), larger average test size and high size variability in *G. subglobosa* Assemblage A may reflect relatively minor dissolution in the lowermost part of the CIROS-1 core from bottom core to ca. 640 mbsf. Accordingly, this stratigraphical interval is characterised by a relatively rich and diversified benthic foraminiferal assemblage (Webb, 1989; Coccioni and Galeotti, 1997).

The smaller-sized populations observed from 520 mbsf to 366 mbsf (i.e. Assemblage B) suggests relatively moderate dissolution. Dissolution of the larger tests may, in fact, account for the presence of uniformly small-sized populations in the upper part of the lower sequence of the CIROS-1 core since, as suggested by Berger (1967), the larger specimens in foraminiferal assemblages would be more vulnerable to dissolution. Accordingly, the intervals where larger tests occur contain better preserved benthic foraminiferal assemblages in the CIROS-1 core. It is possible that the progressively increasing glacial influence in the lower sequence of the CIROS-1 core (see Barrett, 1989) led to increasing dissolution levels through this interval. In particular, similar to what is observed in the present day Ross Sea (see Osterman & Kellogg, 1979), locally higher concentration of CO₂ might have derived from heavy pack-ice concentrations and accompanying low rates of photosynthesis, causing the CCD to occur at shallower depths. However, the consistent presence of agglutinating forms confined to the lower part of the CIROS-1 core (Webb, 1979; Coccioni & Galeotti, 1997) would rather suggest higher dissolution levels characterising this interval.

**CaCO₃ AVAILABILITY**

CaCO₃ availability to the living organisms might also account for the difference in average test size in the two above mentioned populations of *G. subglobosa* from the lower sequence of the CIROS-1 core. A higher CaCO₃ availability would, in fact, produce a range of test sizes (see also Corliss, 1979). However, *S. cf. schreibersiana* shows an increase of test size in the same interval (Figs. 7 &9), which is certainly not compatible with decreasing CaCO₃ availability during deposition of the CIROS-1 core. Under high CaCO₃ solubility conditions, benthic foraminiferal calcareous species become thinner, whereas larger and more robust tests are found as solubility decreases (Scott et al., 1977; Boltovskoy et al., 1991). A mechanism different from either dissolution and/or CaCO₃ availability has, therefore, to be found to explain the observed trends.

**WATER DEPTH**

In line with observation on modern assemblages (see Boltovskoy et al., 1991), water depth might have controlled the morphometric changes shown by the three studied species. However, *G. subglobosa* is reported to develop smaller tests with increasing water depth (see Corliss, 1979). Therefore, the progressive shallowing reported to occur from the bottom core to 366 mbsf in the CIROS-1 drillhole (Hambrey et al., 1989; Webb, 1989; Coccioni and Galeotti, 1997) would have produced a pattern opposite to that observed. Besides this, the genus *Stainforthia* is reported to have a better developed biserial stage (and therefore to become more tapered) at deeper sites (Plum and Freirichs, 1976). The development of more suggestive *S. cf. schreibersiana* in the lower sequence of the CIROS-1 core is a further indication that water depth was not an important factor in controlling the observed morphometric changes in these species.

**ICE COVER-RELATED FACTORS**

The increasing glacial influence observed in the lower sequence of the CIROS-1 core (Barrett et al., 1989) might have led eventually to formation of sea ice. In turn, this may have caused the formation of hypersaline bottom waters, similar to the High Salinity Shelf Water in the present-day Ross Sea (Jacobs et al., 1985). Changing salinity might have played a role in controlling the size changes observed in *S. cf. schreibersiana* and *G. subglobosa* in the CIROS-1 core. In particular, increased bottom water salinity might have counteracted the effect of high CO₂ concentrations on CaCO₃ solubility levels. However, the effect of salinity was not predominant. Although accounting for the development of larger test size in *S. cf. schreibersiana*, higher salt concentrations do not explain the size reduction observed in *G. subglobosa* through the lower sequence of the CIROS-1 core.

The formation of sea ice and hypersaline bottom water would have led to decreased primary productivity, which, in turn, might have influenced benthic foraminiferal test size changes. As reported by Bradshaw (1957, 1961), non-optimal environmental conditions (including low amounts of detritus reaching the sea floor) may result in larger test sizes as found in laboratory studies of *Ammonia tepida*. However, there have been conflicting findings on how low-nutrition may affect benthic foraminiferal size. Lalicker (1948) suggested that insufficient food creates under-sized specimens. The same factor as a probable explanation for small-sized *G. subglobosa* was suggested by Corliss (1979). In contrast, Hallock (1985) reported that nutrition may create slower growth but, in the end, much larger specimens, particularly in reef environments most often associated with algal symbionts. Caralp (1989)
reported that the *M. barleeanus* population from a core collected west of Mauritania developed larger average size and a higher percentage of abnormal individuals when in the presence of abundant organic matter on the sea floor.

More recent data suggest that rapid changes in the flux of organic matter to the sea floor, such as seasonal input of phytodetritus, affect the test size in benthic foraminifera by influencing the reproduction cycle. Changes in test size of benthic foraminiferal species have been reported to occur by Ohga and Kitazato (1997) and Kitazato et al. (2000), from the Sagami Bay, Japan, in response to seasonally influenced organic fluxes to the sea floor. In particular, small-sized tests occur during spring blooms as a response to an acceleration of the reproduction cycle following large food input to the sea floor (Kitazato et al., 2000). The presence of an ice-cover may therefore influence the test size in benthic foraminifera from the studied intervals by creating the conditions for a seasonal pulse of organic matter fluxes to the sea floor. Wollerguth and Kuhl (2000), reported that the mean test size of benthic foraminifera of seasonally ice-free areas, is much larger than in permanently ice-covered areas. Differences in length of life cycles among the three studied species are likely to result in different response to seasonality in downward organic fluxes. Species having a life-cycle longer than one year are likely to have a test growth rate less influenced by seasonal organic input onto the sea floor. Besides changes in test size, the d/D ratio record of *G. subglobosa* from CIROS-1 core, indicates a clear tendency to become smaller and more elongate (uncoiled) from bottom core to 366 mbsf, that is from the late Eocene to the early Oligocene, following the age interpretation of Wilson et al. (1998). This tendency is followed by the first occurrence of *C. parkerianus* which is a common form in the Oligocene upper sequence of the CIROS-1 core where *G. subglobosa* is absent (see Webb, 1989; Coccioni and Galeotti, 1997). *C. parkerianus* is very similar to *G. subglobosa* from which it differs only by having an uncoiled stage in the chamber arrangement. Interestingly, Bandy (1960) observed a remarkable water depth-related trend in the cassidulinids. Limbato, large, sharp-edge species of *Cassidulina*, typical of the inner shell are replaced either by larger globose (such as *G. subglobosa*) or biumbilicate forms at greater depths. Uncoiled forms, such as *Cassidulinoides* and *Ehrenbergina* are typical of bathyal settings.

Following Bandy (1960), the tendency of *G. subglobosa* to uncoil and the subsequent appearance of *C. parkerianus* might reflect increasing water depth and associated changes in environmental conditions, including decreasing organic fluxes and/or temperature. Since the bathymetrical distribution of Recent benthic foraminifera is largely controlled by export production (De Rijk, 2000), changes in the trophic conditions through the lower sequence of CIROS-1 core might have played a central role.

It is interesting to notice that *C. parkerianus* is a rare to common taxon in polar regions (Mead, 1985) but it is virtually absent at lower latitude sites, at least in ODP and DSDP material (see «fossil distribution» at http://www.odsns.de/odns). The presence of an extended hiatus separating the upper Eocene-lower Oligocene lower sequence from the lower-upper Oligocene upper sequence at 366 mbsf in the CIROS-1 core prevents us from verifying whether or not a gradual evolution from *G. subglobosa* to *C. parkerianus* took place. However, since *C. parkerianus* is not known to occur in strata older than the Early Oligocene in the Ross Sea Region, its first evolutionary appearance may be a potential marker that approximates the Eocene/Oligocene boundary at a regional scale.

**TEMPERATURE**

Changes in bottom water temperature have been observed to cause opposite trends in different species in terms of test size (Boltovskoy et al., 1991). Although decreases in bottom water temperature apparently result mostly in increases of benthic foraminiferal test size (Boltovskoy et al., 1991), possibly including *S. cf. schreibersiana*, Corliss (1979) reported that a negative (-0.15) correlation coefficient exists between bottom water temperature and the mean length of *G. subglobosa* in the southern Indian Ocean. Though weak, such negative correlation suggests that *G. subglobosa* would not increase its test size in response to decreasing temperature. Therefore, similarly to fluctuations in trophic conditions (see above), temperature changes might explain the opposite trends observed in the species studied. In particular, lower bottom water temperature may result in smaller-sized *G. subglobosa* and larger-sized *S. cf. schreibersiana*. The presence of very large tests and high size variability in *G. subglobosa* from the Oligocene upper part of the CRP-3 core may be taken as an indication for a return to warmer condition in this interval, following the Eocene-Oligocene transition climate deterioration which accompanied the deposition of the lower sequence of the CIROS-1 core. According to Ehrmann (1987) and Sagnotti et al. (1998), the lowermost part of the CIROS-1 core could represent a relatively warm period. Accordingly, environmental magnetostratigraphical data suggest also that the upper part (at least the uppermost 200 mbsf) of the CRP-3 core would have been characterised by relatively warm conditions similarly to those observed in the lowermost part of the CIROS-1 core (Sagnotti et al., this volume). No clear indications, however, emerge in this regard from the record of *S. cf. schreibersiana*, which shows a progressive increase in
test size average values through the studied interval (Fig. 8).

The uniformly small-sized G. subglobosa population which occurs in a few samples from the lower part of CRP-2/2A core might reflect relatively low bottom water temperature. However, the very restricted range of size variability in this interval suggests reworking. Reworking may also explain the poor preservation of assemblages from this interval (Galeotti et al., 2000).

Dissolved Oxygen Content

The concentration of dissolved oxygen on the sea floor is one of the most important factors controlling the distribution of benthic foraminifera. The proportion of different morphotypes within the benthic foraminiferal assemblages has been shown to be related to the state of oxygenation on the sea floor (Kaiho, 1991, 1994). On the other hand, intraspecific morphometric changes may result in the development of smaller tests under dysoxic conditions. Smaller tests have a higher surface-to-volume ratio and are, then, more efficient in myochondrial respiration. The state of oxygenation may have been a factor controlling the morphometric changes observed in the studied species independently from the above-mentioned environmental parameters. In particular, increasing oxygenation associated with decreased temperature might have produced a pattern of increased size in one species and decreased size in another, depending on the sensitivity to one or the other environmental parameters.

Conclusions

1. Morphometric analysis of G. subglobosa showed no consistent trend with time, but data for S. cf. schreiberiana revealed an increase in size from late Eocene (assemblage A) to early Oligocene (assemblages B-D) that was considered significant.

2. A number of processes might explain the size variability observed in S. cf. schreiberiana. Changes in trophic conditions, possibly related to increased seasonality, and bottom water temperature emerge as the most likely factors in controlling the size patterns in the studied species although other variables such as winnowing for specific intervals cannot be ruled out.

3. The morphological changes in these species is quite limited through time, though locally they may have some value in biostratigraphical correlation.

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