Palaeoecology of the biserial planktonic foraminifer *Heterohelix moremani* (Cushman) in the late Albian to middle Turonian Circum-North Atlantic

Alexandra J. Nederbragt a,*, Robert N. Erlich b, Bruce W. Fouke a,1, Gerald M. Ganssen a

a Instituut voor Aardwetenschappen, Vrije Universiteit, de Boelelaan 1085, 1081 HV Amsterdam, Netherlands
b Amoco Production Company, 501 WestLake Park Boulevard, Houston, TX 77253, USA

Received 5 May 1997; accepted 23 April 1998

Abstract

The Cretaceous *Heterohelix moremani* (Cushman) was the only biserial planktonic foraminiferal species from its first appearance in the late Albian up to the Cenomanian/Turonian boundary. Within that time, it increased gradually in abundance relative to other planktonic foraminifera in five Circum-North Atlantic sections. It is generally rare in upper Albian sediments, common in most of the Cenomanian and very abundant in sediments representing the latest Cenomanian Oceanic Anoxic Event. Short-term variations on the overall abundance trend correlate with positive excursions in the bulk carbonate $^{13}$C record. Maximum rain rates of *H. moremani* during OAE2 show that this species was an opportunist that did well in extreme conditions, but its overall distribution indicates that it is not necessarily a marker for very high palaeoproductivity environments. Stable oxygen and carbon isotope measurements on foraminiferal species indicate that *H. moremani* was a surface water dweller at least in part of its geographic range, but incorporated $^{13}$C out of equilibrium with ambient seawater. It is depleted in $^{13}$C relative to other planktonic foraminifera, which is attributed to vital effects related to its opportunistic character. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: palaeoecology; middle Cretaceous; Heterohelicidae; planktonic foraminifera; carbon isotope stratigraphy; Circum-North Atlantic

1. Introduction

Amongst diverse genera of planktonic foraminifera are a number of groups of small sized opportunists with long biostratigraphic ranges, but with a patchy distribution in time and space. Mid-Cretaceous to Recent triserial forms (*Guembelitria* Cushman and *Gallitella* Cushman), mid-Cretaceous and Cenozoic biserial species (*Heterohelix moremani* (Cushman) and *Chiloguembelina* spp. and *Streptochilus* spp.) and enroled biserial forms (*Cassigerinella* Pokorny and *Cassigerinelloita* Stork) are of limited use for biostratigraphy, because of their long ranges. In part, their stratigraphic distribution is imperfectly documented, because their small size means that they are easily overlooked (Resig...
and Kroopnick, 1983; Kroon and Nederbragt, 1990; Koutsoukos, 1994). However, their geographic distribution gives important palaeoceanographic information. Abundant occurrences of these forms have been related to extreme or variable surface water conditions as in shelf seas or in upwelling areas (Leckie, 1987; Kroon and Nederbragt, 1990; Li and Radford, 1992); or were interpreted as indicative for the presence of an intense Oxygen Minimum Zone (Resig and Kroopnick, 1983; Boersma and Premoli Silva, 1989).

The biserial planktonic foraminifer *Heterohelix moremani* (Cushman) is an exception in the list of opportunists to the extent that it is the only form to evolve, forming the ancestral stock of diverse Late Cretaceous heterohelicid genera. This small biserial species ranged into the Santonian (Nederbragt, 1991) but from its first appearance in the late Albian until the Cenomanian±Turonian boundary it formed a monospecific genus. Heterohelicids started to diversified during the latest Cenomanian Oceanic Anoxic Event (OAE2). *Heterohelix moremani* was interpreted as an opportunist, with geographic variation in abundance giving palaeoenvironmental information. Leckie (1987) concluded that *H. moremani* is indicative for epicontinental sea deposits; Nederbragt (1991) thought that it was a marker for variable conditions more in general. Yet regional palaeoenvironmental conditions may not be the only control on the distribution of this species. Variation in abundance of *H. moremani* was found to allow for biostratigraphic subdivision of upper Albian to lower Turonian sediments in Venezuela. Keeled biostratigraphic marker species were scarce in these sediments because of extreme surface water conditions. The presence of successively rare, common and abundant biserial planktonic foraminifera was used in an unpublished biostratigraphic study to distinguish, respectively, upper Albian, lower and middle Cenomanian and upper Cenomanian or younger sediments.

The aim of this study is to document the geographic and stratigraphic distribution of mid-Cretaceous biserial planktonic foraminifera in order to evaluate their significance for biostratigraphy and (or) palaeoceanography. If *H. moremani* is primarily a palaeoenvironmental indicator then any biostratigraphic zonation using this form, as was done for the Venezuelan sections, is at best regional and biostratigraphic boundaries are potentially diachronous. Conversely, its palaeoceanographic usefulness would be limited if variation in abundance is synchronous over a wide area covering different environments. For this study, distribution patterns of late Albian to early Turonian heterohelicids were documented quantitatively in Circum-Atlantic sections that can be fitted in a standard planktonic foraminiferal zonation. In addition, stable oxygen and carbon isotopes were measured on *H. moremani* and other foraminiferal species, to establish their position in the water column, and to compare their ecology to triserial and Cenozoic biserial planktonic foraminifera.

2. Material and methods

Distribution patterns of *H. moremani* were compiled from washed residues from marl samples as well as thin-sections from limestones from four land sections and one Deep Sea Drilling Project (DSDP) section (Fig. 1). Samples from two more DSDP sites were added for stable isotopes measurements on individual species. To obtain washed residues, marly samples were dried overnight at 50°C, soaked in water, and rinsed over a 45 μm sieve preferably, as only a small part of a *H. moremani* population is large enough to be retained in a 63 μm sieve. Samples from all three DSDP sites and from part of the Monjas section (Spain) consist of weakly consolidated sediments that could be washed over a 45 μm sieve. However, marly samples from the Mellegue section (Tunisia) and some samples from the Monjas section are more consolidated and were washed over a 63 μm sieve. Keeled biostratigraphic marker species were scarce in these sediments because of extreme surface water conditions. The presence of successively rare, common and abundant biserial planktonic foraminifera was used in an unpublished biostratigraphic study to distinguish, respectively, upper Albian, lower and middle Cenomanian and upper Cenomanian or younger sediments.

The aim of this study is to document the geographic and stratigraphic distribution of mid-Cretaceous biserial planktonic foraminifera in order to evaluate their significance for biostratigraphy and (or) palaeoceanography. If *H. moremani* is primarily a palaeoenvironmental indicator then any biostratigraphic zonation using this form, as was done for the Venezuelan sections, is at best regional and biostratigraphic boundaries are potentially diachronous. Conversely, its palaeoceanographic usefulness would be limited if variation in abundance is synchronous over a wide area covering different environments. For this study, distribution patterns of late Albian to early Turonian heterohelicids were documented quantitatively in Circum-Atlantic sections that can be fitted in a standard planktonic foraminiferal zonation. In addition, stable oxygen and carbon isotopes were measured on *H. moremani* and other foraminiferal species, to establish their position in the water column, and to compare their ecology to triserial and Cenozoic biserial planktonic foraminifera.
assemblage, only biserial *Heterohelix* and triserial *Guembelitria* were counted separately from all other planktonic foraminifera.

Sections in Venezuela and near Cismone, NE Italy, as well as part of the Monjas and Mellegue sections consist of limestones, from which thin-sections were made. Numbers of foraminifera and their fragments, calcispheres and radiolaria per surface area were estimated by counting all microfossils in subsequent fields of view, until at least 150 specimens were counted. To estimate percentages of biserial versus spiral planktonic foraminifera, each thin-section was further scanned until around 100 specimens were found that could be positively identified as either biserial or spirally coiled. Triserial planktonic forms cannot be recognised consistently enough to give good estimates of their abundance in thin-section.

All samples were scanned for the presence of biosтратigraphic marker species, and are zoned following the zonation of Caron (1985) with minor modifications. The *Rotalipora subticinensis* Zone and *Rotalipora ticinensis* Zone are combined into a single *R. ticinensis*–*subticinensis* Zone. The name *Rotalipora globotruncanoides* is used as a senior synonym of *Rotalipora brotzeni*. The studied sections together cover the upper Albian to middle Turonian. *Heterohelix moremani* is the only biserial planktonic species until the Cenomanian/Turonian boundary. *Heterohelix globulosa* (Ehrenberg), which has its first appearance near this boundary, is frequent in Turonian samples. *Heterohelix globulosa* differs from *H. moremani* in having larger chambers, which increase more rapidly in size through ontogeny, and in being covered with distinct costae (Nederbragt, 1991). However, intermediate forms are present, and the two species cannot be distinguished consistently in thin-section. They are therefore counted together, giving the abundance of heterohelicids as a group relative to all other planktonic foraminifera.

Carbon isotope stratigraphy offers a tool for correlation in addition to biostratigraphic data, as the pattern of variation in stable carbon isotope composition of pelagic carbonates during the mid-Cretaceous is well documented. Three positive excursions have been recorded in the upper Albian to Turonian (Jenkyns et al., 1994; Erbacher et al., 1996). A nearly 1‰ excursion in $\delta^{13}C$ occurred around the Albian/Cenomanian (A/C) boundary, a brief 0.5‰ $\delta^{13}C$ excursion is found spanning the Cenomanian *R. reicheli* Zone, and a $>2‰$ $\delta^{13}C$ excursion marks the start of the latest Cenomanian OAE2. For stratigraphic purposes, carbon and oxygen isotopes were measured on bulk sediments for limestone as well as marly samples, to ensure compatibility of data for different lithologies. Some 100 mg of powder was drilled from hard limestone samples; for less con-
solidated sediments approximately 0.5 g of material was ground in a mortar.

In addition, stable oxygen and carbon isotope measurements were done on individual planktonic foraminiferal species, to determine the position of *H. moremani* in the water column. Although morphologic preservation of foraminifera in washed residues from the land sections and at DSDP Site 547 is good, specimens are calcite-filled and unlikely to give reliable stable isotope data for individual species. Therefore, additional samples from DSDP Sites 137 and 551, which contain air-filled foraminifera, were used for measurements on individual species. All isotope measurements were done on a Finnigan MAT 251 mass spectrometer with an automated sample preparation line. Samples were dissolved in 100% phosphoric acid at 70°C. Measurements are reported in the standard \( \delta \) notation relative to the PDB standard. Average values are shown for duplicate measurements. Analytical precision of an internal carbonate standard, as well as of duplicated bulk sediment samples, is better than 0.10\( \% \) (1\( \sigma \)) for oxygen and 0.05\( \% \) (1\( \sigma \)) for carbon.

3. Results

3.1. Chimana and Querecual formations, eastern Venezuela

Deposition during the Albian–Turonian in eastern Venezuela consisted mostly of outer shelf to upper slope sediments of the Chimana Formation, and upper slope sediments of the organic carbon-rich Querecual Formation (Hedberg and Pyre, 1944; Alberdi and Lafargue, 1993). The Chimana consists of about 800 m of shales with thin sandstone and limestone interbeds, and is apparently transitional and conformable with the overlying 750 m thick siliceous limestones and shales of the Querecual; the contact between the two formations is diachronous (Dirección de Geología, 1970; Yoris, 1990).

Samples for this study were taken from four locations in eastern Venezuela (including the type localities), and represent a characteristic vertical sequence through both units. The sections were studied as part of an industrial project. Stratigraphic variation in percentages of heterohelicids in the planktonic foraminiferal assemblages is shown in Fig. 2. Age-assignments were tentative, based on scattered occurrences of *Ticinella* spp., which range to approximately the top of the upper Albian, and of large globular *Whiteinella* specimens that are typical for the latest Cenomanian OAE2 and younger Turonian sediments (Caron, 1985). Carbon isotope data do not offer further means for correlation as original values have been altered (Fig. 2). Highly negative \( \delta^{18}O \) values indicate that diagenesis played an important role. In addition, Querecual samples have high organic carbon content, and exchange with the light carbon isotopes of organic material may also have altered the \( \delta^{13}C_{\text{carbonate}} \) signature (Scholle and Arthur, 1980).

3.2. DSDP Site 547, off Morocco

A 350 m thick sequence of dark grey hemipelagic clays, in the lower part interbedded with mud breccias, was drilled at DSDP Site 547 (Hinz et al., 1984). Samples were taken in hemipelagic clays throughout the section, avoiding mud breccias where present. Leckie (1984) assigned the sediments to the upper Albian *R. ticinensis* Zone to middle Cenomanian *Rotalipora cushmani* Zone. However, the presence of *R. cushmani* in the upper part of the section could not be confirmed in this study, and the top of the section is considered to belong to the lower Cenomanian *Rotalipora globotruncanoides* Zone. An early Cenomanian age is supported by stable carbon isotope stratigraphy. The section shows an expanded positive excursion in \( \delta^{13}C \) around the Albian/Cenomanian boundary (Fig. 3), but the top of the section records at best only the base of the next younger, mid-Cenomanian excursion, which would be expected to be present completely if the section extended into the *R. cushmani* Zone (Jenkyns et al., 1994).

Foraminifera are calcite-filled in almost all samples, but faunas show good to excellent morphologic preservation, with low degrees of fragmentation of planktonic foraminiferal tests (Fig. 3). Leckie (1984, 1987) found that *H. moremani* is rare in the >63 \( \mu \)m sieve fraction. The species is much more abundant in the >45 \( \mu \)m sieve fraction, reaching frequencies of more than 20%, but the stratigraphic pattern of variation is similar to that in the >63 \( \mu \)m fraction as analysed by Leckie (1987). *Heterohelix more-
Fig. 2. Percentage of heterohelicids within the planktonic foraminiferal faunas in thin-sections from two eastern Venezuelan sections in the Querecual and Chimana formations, with bulk carbonate δ¹³C values. Note that samples are in stratigraphic order but that thickness is not on a linear scale. Scattered, low δ¹³C values in combination with δ¹⁸O values ranging between −6 and −12‰ (not shown) indicate that stable isotope values are altered.

**mani** is very rare in most of the upper Albian, but shows a first increase in abundance at the base of the A/C δ¹³C excursion. Percentages are variable higher in the section, but a second increase in overall abundance occurs above the excursion. Triserial *Guembelitria* shows a more or less reversed pattern. It is abundant up to the top of the δ¹³C excursion, and very rare above it. Within the excursion, high frequencies of *Guembelitria cenomana* tend to correspond to low frequencies of *H. moremani* and vice versa. Calcispheres, which are the only microfossils other than foraminifera in the Site 547 washed residues, have a scattered distribution throughout the section (Fig. 3).

### 3.3. Monjas section, SE Spain

Upper Albian and upper Cenomanian samples were collected from a section exposed in the Arroyo del Campillo de las Monjas, North of Velez Blanco in southeastern Spain; locality details are described by Jansen et al. (1984). A thick sequence of Aptian/Albian clays and marly clays, which is exposed semi-continuously, is followed by a thin interval of upper Cenomanian marl–limestone alternations, and then by Turonian siliceous limestones. A black shale interval at the Cenomanian/Turonian boundary is absent. The boundaries between the lithologic units correspond to hiatuses (Fig. 4). The absence of δ¹³C excursions is consistent with the presence of hiatuses that were recognised from sedimentologic and biostratigraphic data.

Microfossils other than foraminifera are extremely rare in our samples, except for one sample with abundant radiolaria in the Turonian siliceous limestones (Fig. 4). Comparison of 45 µm and 63 µm sieve fractions shows that a large portion of the total number of *H. moremani* is not retained in the >63 µm sieve fraction, but both fractions give similar patterns of stratigraphic variation. The oldest *H. moremani* are found near the base of the upper Albian *R. ticinensis–subticinensis* Zone, and a first increase in frequencies occurs within the *Rotalipora appenninica* Zone. Above that, the relatively low number of samples, and the presence of hiatuses allow only for recognition of moderately high percentages of *H. moremani* in Cenomanian samples, and high frequencies of heterohelicids as a group...
Fig. 3. Faunal composition in the >45 μm sieve fraction of samples from DSDP Site 547 with bulk carbonate $\delta^{13}$C record. Shaded areas give faunal estimates for each sample, thick lines show a three-point moving average to emphasise general trend. Horizontal lines trace base and top of $\delta^{13}$C excursion.
in the Turonian. *Guembelitria* specimens were not found in the Monjas samples.

### 3.4. Cismon section, northern Italy

The Cismon section offers a continuous record of upper Albian to Turonian limestones and siliceous limestones deposited in a fully pelagic setting (Channell and Medizza, 1981). The section includes a 0.5 m thick black shale, the Bonarelli level, that represents the latest Cenomanian OAE2. Samples were taken at 1 m intervals throughout the section (Fig. 5). For this study, the standard *R. appenninica* Zone is subdivided into a local *Planomalina buxtorfi* Zone and a younger *R. appenninica* Zone. The two species have similar stratigraphic ranges in other areas (Caron, 1985), but the first occurrence of *R. appenninica* in the thin-sections from the Cismon section is found higher in the stratigraphy than expected from its documented first appearance. Biostratigraphic results from our samples are in general agreement with those presented in Bellanca et al. (1996). Minor differences in the position of zonal boundaries can be attributed to the fact that biostratigraphic results are based on thin-sections, in which diagnostic cuts through marker species are relatively rare, and the statistical chance of finding a zonal marker is small. The pattern of stratigraphic varia-
tion in $\delta^{13}C$ and its correlation with biostratigraphy is in good general agreement with published records (Jenkyns et al., 1994).

Planktonic foraminifera are the most frequent microfossils in the section as a whole, but calcispheres and radiolaria are abundant in various levels. Bellanca et al. (1996) found that radiolarian abundances varied at the scale of orbital cycles. Abundant calcispheres usually occur in levels where severe dissolution occurred, indicated by abundant fragments of planktonic foraminifera (Fig. 5). On the other hand, the amount of radiolaria and percentage of fragments are mostly unrelated, which indicates that high abundances of radiolaria are not the result of enrichment because of dissolution of carbonate. Radiolaria disappear from our samples in the lowermost Cenomanian at the top of the $A/C$ boundary $\delta^{13}C$ excursion. This could be an artefact of the equal distance sample spacing, if all samples were consistently located in the carbonate rich lithologies within a cyclic pattern of variation in silica content. However, sedimentologic description of the section, shown schematically in Fig. 5, indicates that the scarcity of radiolaria in Cenomanian samples is real, as it corresponds to a decrease in the amount of chert in the section.

*Heterohelix moremani* shows an overall increase in frequencies throughout the section, but with short-term fluctuations (Fig. 5). The percentage of heterohelicids remains on average more or less constant in the upper half of the *R. appenninica* Zone, but is followed by a minor maximum immediately above the $A/C$ boundary excursion in $\delta^{13}C$. At the same level that radiolarian concentrations drop, numbers per unit surface area of heteroheliacids as well as planktonic foraminifera in general increase abruptly. A more pronounced maximum in relative frequencies of *H. moremani* occurs in the middle Cenomanian. The variation in abundance of *H. moremani* does not correlate obviously with the degree of fragmentation in Albian and Cenomanian samples. However, fluctuations in relative frequencies of heterohelicids in Turonian lime-

Fig. 5. Faunal composition in thin-sections from the Cismon section in northern Italy. Dark shaded area for heterohelicids and fragments give estimates for all samples with thick lines showing a three-point moving average to emphasise general trend. Note that percentages of radiolaria, planktonic foraminifera and calcispheres add to 100%. Shaded horizontal bars trace stratigraphic levels of $\delta^{13}C$ excursions.
stones above the Bonarelli level are more likely to be the result of selective dissolution. Low percentages of heterohelicids in the Turonian are found in samples where most foraminifera are dissolved.

3.5. Oued Mellegue, Tunisia

A thick sequence of upper Cenomanian and younger hemipelagic sediments is exposed around the artificial lake in Oued Mellegue, northeastern Tunisia, which is in the centre of a faulted anticline. The section sampled for this study follows a small subsidiary gully west of the lake. The OAE2-interval is represented by a 36 m thick sequence of limestones and marly limestones that contain up to 3% organic carbon, the Bahloul Formation (Burollet, 1956). The ~2.5‰ δ13C excursion starts at the base of the carbonaceous interval (Fig. 6). Estimates based on Milankovitch cyclicity for the duration of the R. cushmani Zone (2.4 Ma; Gale, 1989), the base of which is not exposed in the section, and the Whiteinella archaeocretacea Zone (0.7 Ma; Kuhnt et al., 1997) give maximum accumulation rates of 20 cm/ka for the section as a whole. Other time scales would give lower values. Correlation of the carbonaceous interval in the Mellegue section with the Moroccan Tarfaya basin (Kuhnt et al., 1990, 1997) indicate that the carbonaceous Bahloul Formation represents accumulation rates of approximately 10 cm/ka, which rates are up to twice as low as in the section as a whole.

The large number of samples from marls as well as limestones allow for a comparison of faunal counts in washed residues (>63 μm fraction) and in thin-section (Fig. 6). The two preparation methods give similar relative frequencies in Cenomanian sediments. Above that, thin-sections give persistently lower estimates of heterohelicid percentages than washed residues for Turonian samples. Presumably, the change from Cenomanian faunas to lower Turonian faunas with abundant H. globulosa and large, globular Whiteinella spp. affect estimates of the percentage of biserial specimens in thin-section in a systematic way.

Heterohelicids reach their maximum abundance within the Bahloul Formation, but relative frequencies vary with lithology within that interval. Heterohelicids are relatively rare in marly, bioturbated levels, which contain abundant fragments (Fig. 6), indicating that dissolution of carbonate occurred. In contrast, planktonic foraminiferal faunas in laminated limestones in the middle of the interval are much better preserved, with less severe dissolution indicated by low amount of fragments. These laminated beds contain the highest concentration of heterohelicids in the section, with spiral planktonic foraminifera forming less than 30% of the planktonic foraminiferal assemblages generally.

As far as can be seen from thin-sections, Hedbergella spp. are the only other species accompanying heterohelicids in the black shale samples. Yet high percentages of heterohelicids in the OAE2 interval cannot be explained as relative enrichment, resulting from the disappearance of almost all other planktonic foraminiferal species. Concentrations of foraminifera in thin-sections can be converted to a relative measure of rain rates, by multiplication with accumulation rates. High relative frequencies of heterohelicids in laminated layers (Fig. 6) correspond to an increase in absolute numbers per unit time, even if accumulation rates for the Bahloul Formation were twice as low as in the rest of the section. Lower fluxes in bioturbated levels with abundant fragments could be primary, but dissolution of a large portion of the planktonic foraminifera reaching the seafloor as the main cause cannot be excluded.

3.6. Compilation of stratigraphic trends

To compare stratigraphic trends, percentages of heterohelicids in the four well-dated sections are plotted against numeric time (Fig. 7). No correction is made for sample preparation methods, which means that actual values cannot be compared directly. Comparison of the 45 μm and 63 μm sieves used for the Monjas samples and comparison of our results for Site 547 with those of Leckie (1987) show that samples washed over a 45 μm sieve give a higher percentage of H. moremani. Cenomanian thin-sections from the Mellegue section give similar values as >63 μm washed residues, i.e. are underestimating the real proportion of biserial specimens. In theory, even the smallest foraminifera should be visible in thin-section, but morphology determines what proportion of specimens is recognisable. Spiral forms can be recognised as such from any cut in thin-
Fig. 6. Faunal composition in thin-sections (open circles) and >63 µm washed residues (black dots) from the Mellegue section, Tunisia.
Fig. 7. Combined heterohelicid abundance records plotted against numeric time scale of Haq et al. (1987).

3.7. Planktonic foraminiferal oxygen and carbon isotopes

Stable isotope measurements were done on *H. moremani* and other species in two samples each from DSDP Sites 137 and 551. Samples from DSDP Site 137 are from the early Cenomanian *R. brotzeni* Zone, while sediments included from Site 551 belong to the upper part of the *R. cushmani* Zone (late Cenomanian). Foraminifera are air-filled, but foraminiferal tests show variable extent of recrystallisation, with addition of some secondary calcite (Plates I and II). Isotope results are shown in Table 1 and Fig. 8. *Het-
erohelix moremani is close to Hedbergella delrioensis and to bulk sediment in $\delta^{18}O$ values in all four samples, but the order relative to keeled species varies. The $\delta^{18}O$ contrast amongst planktonic forms is weak at Site 137, but H. moremani is the lightest (warmest) in oxygen isotopes of all planktonic foraminiferal species in both samples. It has intermediate $\delta^{18}O$ values in the Site 551 samples, which show a wider range between planktonic foraminiferal species. The pattern in $\delta^{18}C$ values is more consistent. Irrespective of its $\delta^{18}O$ signature, H. moremani is lighter in $\delta^{18}C$ than all other planktonic foraminifera except Guembelitria cenomana, and close to benthic foraminifera. Light $\delta^{13}C$ values were also found for Cenozoic biserial planktonic foraminifera and Palaeogene triserials (Resig and Kroopnick, 1983; Boersma and Premoli Silva, 1989). For further comparison, the $\delta^{13}C$ value of the modern triserial, Gallitellia vivans, in a box core top sample is shown relative to other planktonic foraminiferal species (Table 2). Like mid-Cretaceous Guembelitria, G. vivans is the most depleted in $\delta^{13}C$ of all planktonic foraminifera, even though its $\delta^{18}O$ signature shows that this species built its test not far below the sea surface.

4. Discussion and conclusions

4.1. Temporal abundance trends

All studied sections show an overall increase in abundance of H. moremani from its first appearance in the lower R. ticinensis/subticinensis Zone up to the Cenomanian/Turonian boundary. Heterohelicids are generally rare up to the uppermost Albian, then common to moderately abundant until the uppermost Cenomanian, and very abundant from the base of the uppermost Cenomanian OAE2. During the anoxic event, Heterohelix started to diversify, and heterohelicids remained an abundant part of planktonic foraminiferal faunas until the end of the Cretaceous (Nederbragt, 1991). The pattern of variation in the mid-Cretaceous confirms that biostratigraphic interpretation of heterohelicid abundance in Venezuelan sections (Fig. 2) is a good approximation, but the relatively small number of samples does not allow for further refinement of age-interpretations. More precise correlation with other areas might be possible from high-resolution sampling. Although actual abundance values within a given time interval vary between sections, the results give some indication that not only long-term but also short-term fluctuations could be synchronous over a wider area. For example, H. moremani is more frequent in the upper Albian in the Cismon section than in age equivalent samples from DSDP Site 547, but trends in the lower Cenomanian appear to be parallel (Fig. 7). The sections included in this study are all from low to mid-latitudes in the Circum-North Atlantic. Further documentation would have to show if the trend in abundance of H. moremani was global.

4.2. Stable isotope signature and habitat

Faunal variation that is synchronous over a wider area implies that it is the result of large-scale changes

PLATE I
Black bars are 20 µm; white bars with transmitted light photos are 100 µm.
1–6. Heterohelix moremani (Cushman).
1. Sample DSDP 137-11-4, 104–108 cm, lower Cenomanian. Note extensive recrystallisation, with addition of calcite indicated by weakly depressed sutures.
2. Specimen with reniform chambers, sample DSDP 547A-41-1, 58–61 cm, lower Cenomanian.
3. Specimen with globular chambers, Mellegue section sample 96Me20, upper Cenomanian.
4. Edge view of ideotypic specimen, Mellegue section sample 96Me5, middle or upper Cenomanian.
5. Side view of ideotypic specimen, Mellegue section sample 96Me5.
6. Specimen transitional to H. globulosa in having faint costae, Mellegue section sample 96Me20, upper Cenomanian.
7. Transmitted light photo of sample with 25% heterohelicids (two clear specimens indicated by arrows), Cismon section sample 94Cis106, lower Cenomanian.
8. Sample from CTBE interval in Mellegue section with dominant heterohelicids, sample 96Me74.
9. Thin-section with Heterohelix globulosa, arrow points to specimen with proloculus and all other chambers visible, Mellegue section sample 96Me123, lower Turonian.
Table 1
Single species stable isotope measurements in mid-Cretaceous samples

<table>
<thead>
<tr>
<th></th>
<th>137-10-3, 136–138 cm</th>
<th>137-11-4, 104–108 cm</th>
<th>551-6-1, 43–45 cm</th>
<th>551-6-2, 15–18 cm</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>δ¹³C</td>
<td>δ¹⁸O</td>
<td>δ¹³C</td>
<td>δ¹⁸O</td>
</tr>
<tr>
<td>Bulk (powdered sediment)</td>
<td>1.93</td>
<td>−3.52</td>
<td>1.97</td>
<td>−3.03</td>
</tr>
<tr>
<td><em>Guembelitria cenomanana</em></td>
<td>0.89</td>
<td>−1.50</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Hedbergella delrioensis</em></td>
<td>1.83</td>
<td>−3.41</td>
<td>1.96</td>
<td>−3.06</td>
</tr>
<tr>
<td><em>Hx. moremani</em> (45–63 μm)</td>
<td>−0.53</td>
<td>−4.08</td>
<td>0.01</td>
<td>−3.30</td>
</tr>
<tr>
<td><em>Praeglobotruncana</em> spp.</td>
<td>1.90</td>
<td>−3.65</td>
<td>1.97</td>
<td>−3.13</td>
</tr>
<tr>
<td><em>Rotalipora gandolfi</em></td>
<td>1.55</td>
<td>−3.51</td>
<td>1.55</td>
<td>−2.66</td>
</tr>
<tr>
<td><em>Rotalipora cushmani</em></td>
<td></td>
<td></td>
<td>0.22</td>
<td>−2.00</td>
</tr>
<tr>
<td>Mixed benthic foraminifera</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

% *Hx. moremani* (>45 μm) 9.6 5.3 12.7 17.6

in ocean circulation. Information about the habitat of *H. moremani* should give an indication where in the water column changes must have occurred to be able to affect the distribution of this species. If the relative order of species in δ¹⁸O values is taken at face value, then it should be concluded that the depth at which *H. moremani* lived was variable. Values measured here (Table 1) are in a range that was considered primary and representative of sea surface water temperatures by Sellwood et al. (1994), but that was interpreted as the result of diagenetic alteration by Killingly (1983). Here, no attempt is made to solve if absolute δ¹⁸O values are primary or not. Diagenesis can cause a systematic shift especially in oxygen isotope values, but in general the relative order between species remains preserved (Killingly, 1983; Schragg et al., 1992). However, the small, thin-walled test of *H. moremani* has a large surface-to-volume ratio, and precipitation on the wall surface of secondary calcite (Plate II) would have a larger impact on the measured stable isotope composition than in other species with thicker shells. Cenomanian sediments at DSDP Sites 137 and 551 are amongst the best preserved available (Sellwood et al., 1994), but preservation is by no means perfect. Cenomanian sediments at Site 551 were deposited on top of oceanic basement, and interaction with basement fluids could have caused size dependent enrichment in δ¹⁸O. On the other hand, interspecies contrast in stable oxygen isotopes at Site 137 are too small to allow for conclusive depth-ranking of planktonic foraminiferal species, even if values are not altered. However, a surface water habitat for *H. moremani* in at least part of its range is supported by its abundance in shallow water deposits (Leckie, 1987). The light δ¹³C values found for biserial and triserial forms are more conclusive. The favoured explanation here is that *H. moremani* was most likely

**PLATE II**

Bar is 5 μm.

1. Detail of external wall structure of *H. moremani* specimen in Plate I, fig. 1, Sample DSDP 137-11-4, 104–108 cm, lower Cenomanian.
2. Detail of *H. delrioensis* specimen from which ultimate chamber was removed, showing moderately well preserved wall but with minor secondary calcite on outer and inner wall surfaces, Sample DSDP 137-11-4, 104–108 cm, lower Cenomanian.
3. Detail of moderately well preserved wall structure of *R. cushmani* specimen, Sample DSDP 137-11-4, 104–108 cm, lower Cenomanian.
4. Broken *H. moremani* specimen, showing extensive recrystallisation and addition of secondary calcite. Note large euhedral calcite crystal on the right. Sample DSDP 551-6-1, 43–35 cm, upper Cenomanian.
5. Broken *H. delrioensis* specimen showing recrystallisation, Sample DSDP 551-6-1, 43–35 cm, upper Cenomanian.
6. Partly recrystallised wall structure of broken *R. cushmani* specimen, with minor growth of crystals on inner surface, Sample DSDP 551-6-1, 43–35 cm, upper Cenomanian.
a surface dweller, maybe lived in deeper waters in some parts of its geographic range, but that it was depleted in $^{13}$C independent of its position in the water column.

Depletion in $^{13}$C relative to other planktonic foraminifera is found not only for *H. moremani*, but also for mid-Cretaceous and Palaeogene *Guembelitria* spp. and Cenozoic biserial planktonic foraminifera (Fig. 8; Resig and Kroopnick, 1983; Boersma and Premoli Silva, 1989) and modern *Gallitellia vivans* and *Globigerina bulloides* (Table 2). Cenozoic biserial planktonic foraminifera were heavy in stable oxygen isotopes in most of their stratigraphic range, which led to the hypothesis that these forms build their test in equilibrium with ambient water deep in the water column in an Oxygen Minimum Zone depleted in $^{13}$C (Resig and Kroopnick, 1983; Boersma and Premoli Silva, 1989). However, $^{18}$O values in the two living species from the Banda Sea, *Gl. vivans* and *G. bulloides*, indicate that there is no correlation between their $^{13}$C value and that of ambient water (Table 2). Both species are depleted in $^{13}$C relative to other planktonic foraminifera, for which $^{18}$O values show that they lived at a similar depth in the water column. More extensive data for *G. bulloides* indicate that this opportunistic species incorporates car-
4.3. Palaeoproductivity

Even if an opportunist, *H. moremani* is not necessarily a straightforward palaeo-high-productivity indicator. An obvious tracer for any relation between variation in abundance of this species and surface water productivity would be to measure the $\delta^{13}C$-contrast between planktonic and benthic foraminifera in a deep water section. However, such a record would be hard to obtain in practice, as few, if any, mid-Cretaceous deep water sections are well enough preserved to establish a continuous stratigraphic record of $^{13}C$ measurements on individual species. But sedimentologic and faunal data offer some indication that increased abundances of *H. moremani* during the Cenomanian may correspond to lower productivity overall. At DSDP Site 547 (Fig. 3), the overall increase of *H. moremani* is accompanied by an overall decrease in *Guembelitria*, which was classified as a high-productivity indicator (Kroon and Nederbragt, 1990). In the Cismon section, high abundances in the Cenomanian occur after a distinct decrease in the abundance of radiolaria. In the modern ocean, radiolaria are abundant in areas with high primary productivity. In addition, on a global scale, burial rates of phosphate dropped after a distinct decrease in the abundance of radiolaria (Föllmi, 1996), which, since phosphate burial is linked to burial of organic matter, may point to an overall decrease in productivity. None of these arguments is conclusive on its own, but taken together they suggest that an increase in abundance of *H. moremani* cannot be interpreted as a straightforward indication of increased palaeoproductivity. *Heterohelix moremani* appears to have been a surface dwelling opportunist, that could withstand extreme conditions. Living planktonic foraminifera thrive at intermediate levels of productivity. Presumably, as an opportunist, *H. moremani* could withstand higher levels of productivity than most other planktonic foraminiferal species. Yet assemblages with abundant *H. moremani* probably represent only moderately high palaeoproductivity. Its abundance variation at DSDP Site 547 and in the Mellegue section correlates with excursions in the stratigraphic $\delta^{13}C$ record. Such positive excursions are attributed to enrichment of the global $^{13}C$ reservoir due to excess burial of organic material, either through increased preservation of organic carbon or through enhanced productivity, or to a combination of the two (Pedersen and Calvert, 1990; Arthur and Sageman, 1994). This indicates a relation with global oceanographic changes, that should be taken into account when interpreting variation in abundance of *H. moremani* on a regional scale.

---

Table 2

<table>
<thead>
<tr>
<th>Stable isotope measurements for modern foraminifera from Banda Sea box core (after Kroon and Nederbragt, 1990)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>GS-2-33B</strong></td>
</tr>
<tr>
<td><em>Globigerina bulloides</em></td>
</tr>
<tr>
<td><em>Globigerinoides trilobus</em></td>
</tr>
<tr>
<td><em>Gallitellia vivans</em></td>
</tr>
<tr>
<td><em>Globorotalia menardii</em></td>
</tr>
<tr>
<td><em>Uvigerina perigrina</em></td>
</tr>
<tr>
<td><em>Globobulimina pacifica</em></td>
</tr>
</tbody>
</table>

---

Other planktonic foraminiferal species also have a light $\delta^{13}C$ signal initially, which was attributed to higher metabolic rates in juveniles (Berger and Vincent, 1986; Kroon and Darling, 1995). A light $\delta^{13}C$ signature as a result of rapid growth in *G. bulloides* throughout its life span is consistent with the fact that this species is an opportunist that proliferates in high-productivity areas. Mid-Cretaceous biserial and triserial planktonic foraminifera are similar to *G. bulloides*, in that the their $\delta^{13}C$ values are consistently lighter than other planktonic groups with nearly the same $\delta^{18}O$ value. Most likely, their light $\delta^{13}C$ signature reflects ‘vital effects’ as those in *G. bulloides* rather than chemical composition of the ambient water. It is tempting to equate such a light $\delta^{13}C$ signature in fossil species with an opportunistic life style.

There can be little doubt that *H. moremani* was an opportunist. It had maximum abundance during the latest Cenomanian OAE2, when most other spiral planktonic foraminifera were greatly reduced in numbers or, in the case of *Rotalipora* species, had become extinct. Data from the Mellegue section (Fig. 6) show that the increase in percentages within the population were not only the result of disappearance of other forms. *Heterohelix moremani* was not merely surviving, but the increase in fluxes indicates that it was actually thriving.
Acknowledgements

We are grateful to J.E. van Hinte, D. Kroon, I. Premoli Silva and F. Robaszynski for suggestions for improving earlier versions of the manuscript. Thanks are due to shipboard crew and onshore staff of DSDP and ODP for making part of the samples available. S. Kars made the S.E.M. photographs. This is a publication of the Netherlands Research School of Sedimentary Geology.

References


Lipson-Benitha, S., Flexer, A., Rosenfeld, A., Honigstein, A., Conway, B., Eris, H., 1990. Dysoxic sedimentation in the...


