

The significance of iron-stained foraminifera off SE Trinidad, West Indies, western central Atlantic Ocean

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Abstract – Eleven samples of seafloor sediment were taken from water depths of 78–90 m within the Savonette Field, off SE Trinidad, western Atlantic Ocean. This surface sediment is relict, having been deposited during an early Holocene transgression. The samples yielded much iron-stained quartz and a rich assemblage of dead foraminifera, of which 75 % of planktonic foraminifera were stained with iron, as was 66.5 % of the calcareous benthonic foraminiferal assemblage. The fauna, both iron-stained and unstained, was dominated by *Cibicidoides* ex. gr. *pseudoungerianus*, and is concluded, despite the proximity of the Orinoco Delta, to be equivalent to a relict *Cibicidoides* biofacies in carbonate-rich areas of the Gulf of Mexico. Staining was by limonite and hematite. Differing percentages of calcareous benthonic species had been stained with iron, ANOVA revealing three groups of species within which the mean percentage of iron-stained specimens per sample did not differ: (a) *Globocassidulina subglobosa* and *Hanzawaia concentrica*; (b) *Amphistegina gibbosa*, *Cassidulina norcrossi australis* *Cibicoides* ex. gr. *pseudoungerianus*, *C. io*, *Elphidium translucens* and *Quinqueloculina lamarckiana*; and (c) *Eponides antillarum* and *E. repandus*. It is concluded that species differ in their susceptibility to iron staining, and that planktonic foraminifera are more susceptible than most benthonic species. Although waters off northern South America are turbid and the photic zone only ~ 25 m deep, the relict assemblage contained 8.4 % algal symbiont-bearing foraminifera (especially *A. gibbosa* and *E. translucens*) that would be limited to the photic zone. These are thought to have lived at a time early in the Holocene transgression when sequestration of sediment within the Orinoco delta rendered the water sufficiently clear for viable populations of symbiont-bearing foraminifera. Should iron-stained foraminifera prove to be restricted to transgressive systems tracts, this would make them a useful sequence stratigraphic tool.

Keywords: Holocene, relict, Orinoco, Amphistegina, transgressive systems tract.

1. Introduction

After the death of any hard-shelled creature, and subsequent to the decay of its soft tissues, its skeletal components become subject to the same sedimentary processes as lithic particles. Among the foraminifera, a proportion of the dead tests may be destroyed by abrasion or dissolution (cf. Kotler, Martin & Liddell, 1992, p. 309), leading to significant changes in the information to be gained from the taphocoenosis as compared to the biocoenosis (Martin & Wright, 1988). The tests of dead foraminifera nevertheless remain useful for studies such as those tracing sediment movement (Chang, 1984; Li, Jones & Blanchon, 1997; Hohenegger, 2000) or the detection of relict sediment on continental shelves (Bandy, Ingle & Resig, 1965; Emery, 1968).

Post mortem chemical alteration of calcareous foraminiferal tests has long been noted. Murray (1967) found that acid water renders transparent tests opaque. Seiglie (1970) recorded abundant altered tests on the neritic Cabo Rojo Platform off SW Puerto Rico and, although he did not present any chemical analyses,

concluded them to comprise glauconite and goethite. He suggested that alteration to glauconite occurs where there is mixing of river- and sea-water, and that the glauconite in altered tests is converted to goethite when washed into agitated, oxic water. Wilson (2006a) hypothesized that altered tests of the miliolid *Archaias angulatus* around the West Indian island of Nevis form in sediment with dysoxic pore water.

Maiklem (1967) recorded terrigenous, iron-stained sediment grains around the Capricorn Reef Complex, Australia, and on adjacent parts of the inner shelf in a zone where terrigenous and carbonate sediments were being mixed. Many of the associated foraminiferal tests were stained by iron and manganese sulphides, hydroxides and oxides. The iron and manganese, Maiklem wrote, were derived from the terrigenous component, and he showed that sulphate-reducing bacteria are re-precipitating these elements under reducing conditions around nuclei of organic material such as foraminiferal tests. Bioturbation (or erosion) brings the reduced sediment back into the oxidizing zone, where the black sulphides oxidize to brown ferric hydroxides and oxides. Batista, Vilela & Koutsoukos (2007) appealed to this mechanism to explain the occurrence of iron-stained benthonic foraminifera around the Parrachos

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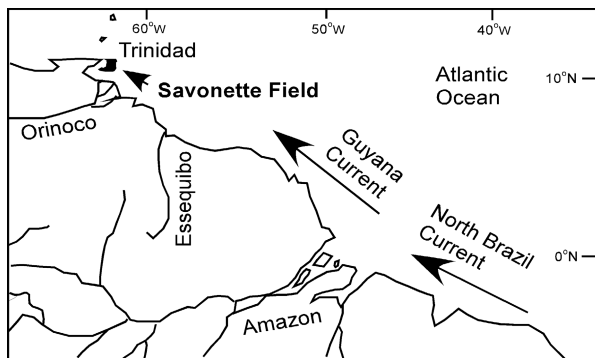


Figure 1. NE South America, showing the locations of the major rivers, the path of the Guyana Current and the Savonette Field.

de Maracajaú Reef, Brazil, while Butcher & Steinker (1979) invoked a similar mechanism to explain the chemical alteration of *A. angulatus*.

Since the end of the last glacial maximum at *c.* 18 ka BP, sea-levels have risen 120–130 m (Poag, 1973). Terrigenous sediment is currently being sequestered in marginal marine areas such that, excepting around prograding deltas, the continental shelves are effectively being starved of terrigenous input. Consequently, ~70% of the shelfal area worldwide is coated with partially or entirely relict sediment deposited in the early stages of the Holocene transgression (Kennett, 1982) in which the foraminiferal assemblage may comprise 80–90% relict tests. There have been several records of chemically altered foraminifera from these deposits (Conolly & Von der Borch, 1967; Andreieff *et al.* 1971; Douglas *et al.* 1980; Bornhold & Giresse, 1985). Vilela (2003) recorded dark and abraded tests in two cores from 70 m water depth on the Amazon Shelf off Brazil. She concluded that these tests were relict.

The studies outlined above examined either individual species (especially *A. angulatus*) or the altered foraminiferal assemblage as a whole. They noted a range of alteration products (iron oxides and sulphides, glauconite and goethite). They did not, however, characterize the components of the altered assemblage in greater detail. During a routine but proprietary examination of live (Rose Bengal-stained) benthonic foraminifera in the Savonette Field area, off SE Trinidad, western Central Atlantic Ocean (Fig. 1; latitude 10°06' N, longitude 60°15' W), many dead foraminiferal tests, both planktonic and benthonic, were found to be stained with either blood-red hematite or yellowish-red limonite, forming an iron-stained calcareous benthonic foraminiferal association (ISCBFA). In association with this iron staining, miliolids showed occasional blackish alteration also, especially along the sutures. This paper examines this ISCBFA in greater detail, compares the proportions of the planktonic and benthonic populations that have been stained with iron, and contrasts the proportions of iron-stained specimens between species within the ISCBFA.

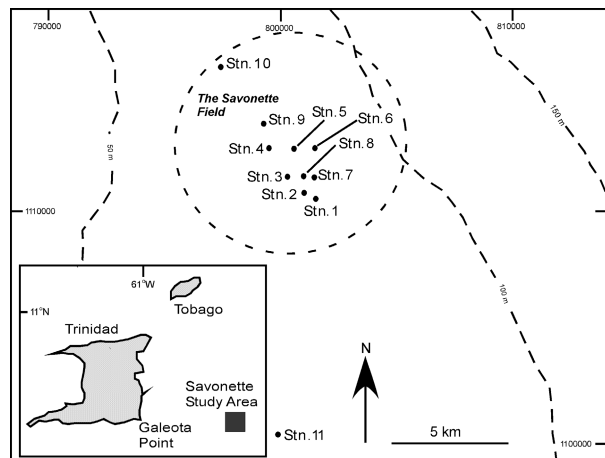


Figure 2. Sample stations within the Savonette Field area. WGS84 Zone 20N Universal Transverse Mercator grid coordinates.

2. Previous work

The continental shelf around Trinidad and NE Venezuela was surveyed sedimentologically by Koldewijn (1958), who noted the sediment of the Savonette area to comprise calcarenitic sandy pelite to very pelitic calcarenite. Carr-Brown (1972) examined the continental shelf east of Galeota Point close to the Savonette Field, using samples collected in water depths of 61–66 m. He concluded that the continental shelf in the area comprises a deltaic Pleistocene succession overlain by a layer of Holocene calcarenitic sandy deposits 0.05–1.6 m thick. On the basis of a radiocarbon date for the Pleistocene deposits, he concluded that the Holocene succession is 'largely composed of reworked Pleistocene sands, laid down approximately 11 500–6000 years ago (relict transgressive facies)'. He assumed that deposition in the area virtually ceased at the end of the early Holocene transgression.

The micropalaeontology of the continental shelf round Trinidad was surveyed by Drooger & Kaasschieter (1958). Their material included samples from two transects (DG and DR) that respectively lie about 30 km SE and NW of the Savonette area. They estimated the total (live + dead) fauna in the Savonette area to comprise 15–20% *Cibicides pseudoungerianus* and vars., ~5% *Eponides antillarum*, 4–5% *Hanzawaia concentrica* and 1–2% *Amphistegina lessonii* (= *A. gibbosa* of this report), an assemblage that Carr-Brown (1972, fig. 2) characterized as indicating a *Cibicides pseudoungerianus* vars. biofacies. Drooger & Kaasschieter (1958) also recorded 1–2% *Elphidium poeyanum*. Given the distance between Drooger & Kaasschieter's (1958) transects and the Savonette region, however, these percentages must be regarded as approximate only.

Wilson (2006b) surveyed the 2005 benthonic foraminiferal fauna from the Ibis Field, about 50 km due west of the Savonette Field. Given that some of Drooger & Kaasschieter's (1958) transects pass

within a few kilometres of the Ibis Field, Wilson (2006b) was confident that the percentage abundances recorded by Drooger & Kaasschieter were in this case an accurate reflection of those in the population. Wilson (2006b) found the total (live + dead) assemblage there to differ markedly from that reported by Drooger & Kaasschieter (1958), with overall increases in the proportional abundances of *Uvigerina subperegrina*, *Ammonia pauciloculata/Rolhausenia rolhauseni* and *Pseudonion atlanticum*. This change in the Ibis area had killed off *Cibicidoides pseudoungerianus* and *Miliolinella subrotunda* and reduced the relative abundance of *Hanzawaia concentrica*, but had not affected the relative abundance of *Cancris sagra*. That the benthonic foraminiferal assemblage in the Ibis area comprised < 1 % altered foraminifera (Wilson, unpub. data) suggests that alteration is limited to sites further west.

Van der Zwaan & Jorissen (1991) used Drooger & Kaasschieter's (1958) data to recognize six biofacies (Zones) around Trinidad. The Savonette area lies within their Zone VI, which they characterize as occupying a sandy zone little influenced by Orinoco outflow. Wilson (2007, 2008) found ostracod biofacies off SE Trinidad to be arrayed perpendicular to bathymetric contours and concluded that this reflects the interplay of Amazon- and Orinoco-derived water along an estuarine front within the Orinoco Plume. The Ibis and Savonette Fields lay on opposite sides of this front, the Savonette Field being beneath surface water derived from the River Amazon.

3. Materials and methods

Ten samples were recovered from Stations 1–10 within the Savonette Field area, and one further south from Station 11 (Fig. 2). All were taken with a van Veen grab. Water depths at the stations ranged from 78 to 90 m (online Appendix 1 at <http://journals.cambridge.org/geo>). For ease of statistical manipulation, sample locations were recorded as grid references using UTM/WGS84 coordinates.

The material examined from each sample comprised the top 1 cm over an area of 400 cm². Each was washed over a 63 µm mesh to remove silt and clay, and then air dried. The samples had been stained with Rose Bengal to distinguish live foraminifera from dead, but a total of only 253 Rose Bengal-stained benthonic foraminifera were recovered from the entire sample suite. This live assemblage was dominated by *Eponides antillarum* (53 %) with lesser *Marginulinopsis planatus* (32 %). Removal of these few specimens is thought unlikely to have affected the results from the present exercise, which is based on dead foraminifera only. The residue was weighed, then split using an Otto microsplitter to give an aliquot of ≥ 350 dead benthonic foraminifera. All specimens (planktonic + benthonic) were picked to a total of 200 benthonic foraminifera, and this figure used to calculate %p, the percentage of the fauna as planktonic individuals (de Rijk, Troelstra &

Rohling, 1999; Wilson, 2003). The remaining benthonic foraminifera were then picked. All benthonic specimens were sorted into species using Phleger & Parker (1951), Drooger & Kaasschieter (1958), Poag (1981) and Hofker (1983).

Calcareous specimens (miliolids and rotalids) were characterized as being either fresh or iron-stained, the latter comprising the ISCBFA. As the textularids and the agglutinating miliolids might possibly have accumulated iron-stained particles while alive, no attempt was made to distinguish these as iron-stained or fresh, and, once their presence had been noted, they were excluded from any further analyses. Analyses were thus limited to the calcareous benthonic foraminifera, among which the amount of staining varied markedly from a pale patch to deep staining that pervaded the entire test, the latter being especially the case among miliolids. Although an attempt was made to develop a scale reflecting the degree of staining, this was not found to be consistently workable. Thus, a specimen was deemed to be stained with iron if it showed any staining at all. A proportion of the specimens were broken. These might equate to the eroded specimens of *Amphistegina* noted by Hofker (1983). However, Wetmore (1987) having noted that a force as low as 1 N can break a specimen, it was concluded that fragile specimens of the smaller benthonic species might have been broken during sample retrieval and preparation. Thus, no attempt was made to distinguish broken from pristine specimens. To facilitate comparisons, the stained and unstained assemblages were treated as separate sub-assemblages. Their diversity within each sample was calculated using the information function $H = -\sum p_i \ln p_i$. Pearson's product moment correlations between measures were accepted as significant at a level of $p < 0.05$. Although the continental shelf east of Trinidad extends approximately north–south, the shallow depth at the most southerly Station 11 resulted in depth being positively correlated with northings ($r = 0.77$).

4. Results

The sample residues ranged in mass from 2.1 to 11.0 g (online Appendix 1 at <http://journals.cambridge.org/geo>; mean 5.8 g) and comprised mostly quartz with lesser foraminifera, ostracods, mollusc debris and rare bryozoans. Many of the quartz grains were stained red-brown with ferruginous matter. No pyrite was noted. Residue masses varied randomly throughout the study area, not being significantly correlated with northings, eastings or water depth.

The percentage of the total (iron-stained + unstained) foraminiferal fauna as planktonic specimens (%p) ranged from 18.5 to 57.5 % (mean 32 %) and was significantly correlated with eastings ($r = 0.68$). The planktonic assemblage was co-dominated by *Globigerinoides ruber* and *Globoturborotalita rubescens*, the former of which has a capacity to withstand neritic conditions (Bandy, 1956). A mean of 75 % of the

planktonic foraminifera per sample were iron stained. There was a significant negative correlation between %*p* and the percentage of the planktonic foraminiferal assemblage stained with iron ($r = -0.66$), indicating an eastward decrease in the incidence of staining.

4.a. Characteristics of the total benthonic foraminiferal assemblage

A total of 4293 benthonic foraminifera in 96 species were picked from the samples. Of these, nine species possess agglutinated tests: *Bigenerina irregularis*, *Liebussella arenosa*, *Siphonaperta horrida*, *Spiroglutina glutinosa*, *Spiroplectamina floridana*, *Textularia agglutinans*, *T. luculenta*, *T. pseudotrochus* and *Trochammina* sp. These comprised 189 specimens only (4.4 % of total recovery) and were excluded from further analyses.

The diversity of the total calcareous benthonic assemblage, as measured using the information function *H*, was positively correlated with %*p* ($r = 0.71$). However, it was negatively correlated with the percentage of the planktonic foraminiferal association that had been stained with iron ($r = -0.80$). This reflects a tendency towards an eastward increase in benthonic diversity within the study area.

Of the total assemblage, six species are known to harbour algal symbionts: *Amphistegina gibbosa*, *Amphistegina radiata*, *Elphidium* sp., *E. advenum*, *E. translucens*, *Heterostegina antillarum* and *Peneroplis proteus*. These formed a mean of 8 % of the total calcareous assemblage (range 5–19 % per sample).

4.b. General characteristics of the fresh calcareous benthonic association

The unaltered association of calcareous benthonic foraminifera comprised 1437 specimens in 65 species (online Appendix 1 at <http://journals.cambridge.org/geo>), of which 11 formed > 5 % of the assemblage in any one sample. In rank order of mean percentage abundance per sample these are: *Cibicidoides* ex gr. *pseudoungerianus* (35 %), *C. io* (16 %), *Eponides antillarum* (9 %), *Hanzawaia concentrica* (5 %), *Globocassidulina subglobosa* (4 %), *Amphistegina gibbosa* (4 %), *Cassidulina norcrossi australis* (4 %), *Elphidium translucens* (3 %), *Marginulinopsis planatus* (3 %), *Discorbis floridensis* (2 %) and *Eponides repandus* (1 %). The per sample information function ranged from $H = 1.75$ – 2.52 , and was significantly correlated with eastings ($r = 0.75$).

4.c. General characteristics of the iron-stained calcareous benthonic foraminiferal association (ISCBFA)

Of the calcareous benthonic foraminifera, 2667 specimens were iron stained (66.5 % of all calcareous benthonic foraminifera recovered; online Appendix 2 at <http://journals.cambridge.org/geo>). A mean of 65 % of the calcareous benthonic foraminifera in each

sample was iron-stained. This was a significantly lower percentage than the mean 75 % iron-stained planktonic foraminifera (Student's *t*-test, $t_{\text{obs}} = 3.33$, $t_{\text{crit}} = 2.09$, $df = 20$). There was no significant correlation between the percentages of the calcareous benthonic and planktonic foraminiferal assemblages in each sample that were iron-stained. Whereas the percentage of iron-stained planktonic foraminifera increased with eastings, the percentage of the calcareous benthonic assemblage as ISCBFA was correlated with both depth and northings ($r = 0.84$ and 0.81 , respectively).

The ISCBFA comprised 72 species. Ten of these formed > 5 % of the iron-stained assemblage in any one sample. In rank order of mean percentage abundance these are: *Cibicidoides* ex gr. *pseudoungerianus* (33 %), *C. io* (11 %), *Hanzawaia concentrica* (10 %), *Globocassidulina subglobosa* (6 %), *Eponides antillarum* (5 %), *Quinqueloculina lamarckiana* (4 %), *Elphidium translucens* (4 %), *Amphistegina gibbosa* (4 %), *Cassidulina norcrossi australis* (3 %) and *Eponides repandus* (3 %). The percentage per sample of the total calcareous benthonic foraminiferal assemblage as ISCBFA ranged from 48 % at Station 11 to 73 % at Stations 7 and 9. Per sample *H* for the ISCBFA ranged from 2.07 (Station 11) to 2.68 (Station 1), and was positively correlated with depth ($r = 0.61$) and northings ($r = 0.69$). It was also negatively correlated with the percentage of the planktonic assemblages as iron-stained specimens ($r = -0.69$). The information function showed the ISCBFA (mean $H = 2.46$) to be significantly more diverse than the unstained assemblage (mean $H = 2.23$; $t_{\text{obs}} = 2.31$, $t_{\text{crit}} = 2.09$, $df = 20$).

Fifteen altered species within the ISCBFA comprised porcellaneous-walled miliolids, the remainder being hyaline-walled rotalids. Student's *t*-test indicated that the mean percentage of 86 % iron-stained miliolids per sample was significantly greater than the mean of 64 % iron-stained rotalids ($t_{\text{obs}} = 6.05$, $t_{\text{crit}} = 2.09$, $df = 20$). Four genera (*Amphistegina*, *Elphidium*, *Heterostegina* and *Peneroplis*) are known to support algal symbionts, and are thus known to be limited to the photic zone. The mean percentage (68 %) per sample of symbiont-bearing foraminifera that were altered did not differ significantly from the mean percentage of iron-stained foraminifera that do not utilize symbionts (65 %; $t_{\text{obs}} = 0.51$, $t_{\text{crit}} = 2.09$, $df = 20$).

The percentage of each species in each sample stained with iron was calculated. A one-way between-groups analysis of variance was conducted to ascertain if the mean percentage of iron-stained specimens differed among the ten species forming > 5 % of the iron-stained assemblage in any one sample (Table 1). There was a statistically significant difference at the $p < 0.05$ level ($F = 2.59$, $p = 0.01$). The lowest mean percentage iron-stained was for *Eponides repandus* (28.5 %), the highest for *Globocassidulina subglobosa* (71.0 %). Subsequent application of Bonferroni's test for equality of means revealed three groups (a–c) within which the mean percentage stained with iron did not

Table 1. The percentage of specimens stained with iron among the ten species forming > 5 % of the iron-stained calcareous benthonic foraminiferal assemblage in any one sample

| Species | Station 1 | Station 2 | Station 3 | Station 4 | Station 5 | Station 6 | Station 7 | Station 8 | Station 9 | Station 10 | Station 11 |
|---|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|------------|------------|
| <i>Amphistegina gibbosa</i> | 58.3 | 65.0 | 75.0 | 50.0 | 83.3 | 66.7 | 90.0 | 80.0 | 0.0 | 77.8 | 27.5 |
| <i>Cassidulina norcrossi australis</i> | 37.5 | 76.9 | 63.2 | 44.4 | 42.1 | 50.0 | 77.8 | 75.0 | 57.1 | 75.0 | 0.0 |
| <i>Cibicidoides ex gr. pseudoungerianus</i> | 57.1 | 65.3 | 64.3 | 65.0 | 64.6 | 77.4 | 69.2 | 51.2 | 68.3 | 58.2 | 56.3 |
| <i>Cibicidoides io</i> | 56.5 | 62.1 | 49.3 | 64.3 | 49.2 | 67.9 | 62.7 | 61.0 | 54.9 | 60.0 | 20.0 |
| <i>Elphidium translucens</i> | 58.3 | 62.5 | 65.5 | 75.0 | 73.7 | 46.2 | 78.6 | 90.0 | 83.3 | 83.3 | 0.0 |
| <i>Eponides antillarum</i> | 64.3 | 51.2 | 38.9 | 53.5 | 57.1 | 60.0 | 76.5 | 0.0 | 53.8 | 37.5 | 31.8 |
| <i>Eponides repandus</i> | 81.8 | 76.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 63.6 | 0.0 | 0.0 | 91.7 |
| <i>Globocassidulina subglobosa</i> | 78.6 | 61.1 | 80.8 | 80.0 | 64.0 | 52.9 | 80.0 | 50.0 | 80.6 | 70.8 | 81.8 |
| <i>Hanzawaia concentrica</i> | 75.8 | 78.0 | 62.9 | 83.8 | 84.4 | 85.1 | 0.0 | 57.7 | 84.6 | 88.5 | 66.7 |
| <i>Quinqueloculina lamarckiana</i> | 0.0 | 83.3 | 88.9 | 77.8 | 87.5 | 85.7 | 87.5 | 0.0 | 0.0 | 0.0 | 62.5 |

For sample station locations, see Figure 2.

differ (in rank order, highest first): (a) *G. subglobosa* and *H. concentrica*; (b) *E. translucens*, *C. ex gr. pseudoungerianus*, *A. gibbosa*, *C. io*, *C. norcrossi australis* and *Q. lamarckiana*; and (c) *E. antillarum* and *E. repandus*.

5. Discussion

At the Savonette Field the total dead (fresh + iron-stained) calcareous benthonic foraminiferal assemblage in its entirety comprised 33 % *Cibicidoides ex gr. pseudoungerianus*, 13 % *C. io*, 8 % *Hanzawaia concentrica*, 7 % *Eponides antillarum*, 4 % *Amphistegina gibbosa* and 3.5 % *Elphidium translucens*. (Section 4.b lists the mean values per sample across the sample suite.) This differed markedly from the live fauna, which was dominated by *E. antillarum* with lesser *Marginulinopsis planatus*. It is not known if this difference is due to a change in the overall composition of the fauna over time, or to transient blooms in the two dominant, live species.

Drooger & Kaasschieter (1958) produced a series of maps on which they used relatively widely spaced transects to depict the suggested distributions of selected species in the early 1950s. The percentage abundances that Drooger & Kaasschieter (1958; see Section 2 above) recorded in the Savonette Field area for *Cibicidoides pseudoungerianus* vars., *H. concentrica*, *E. antillarum*, *A. gibbosa* (as *A. lessonii*) and *Elphidium* (as *E. poeyanum*) differ somewhat from those recorded here, *Cibicidoides ex gr. pseudoungerianus* in particular being recorded much more abundantly in the present study. Wilson (2006b) used changes in the percentage abundance of species within the Ibis Field to suggest that organic matter loading in that area had increased markedly over the past 50 years. However, the transects on which Drooger & Kaasschieter (1958) based their figures were far from the Savonette Field, allowing little confidence to be placed in the percentage abundances they suggested for the Savonette area. For this reason, the differences between the percentage abundances recorded here and by Drooger & Kaasschieter (1958) need not reflect the

degree of recent environmental change in Savonette Field.

Live *Amphistegina* are symbiotic with algae that restrict their occurrence to the photic zone (Reiss & Hottinger, 1984; Hallock, 2000). Hofker (1983) reported from Secchi disc observations off Guyana and Surinam (~ 500 km SE of Trinidad) that the photic zone, the illuminated surface layer of the ocean (Tett, 1990), extends down to 25 m only. Recording abundant *Amphistegina gibbosa* in that area at depths of 80–100 m, he concluded them to be relict. The Savonette Field currently lies in water 78–90 m deep. The water around Trinidad can be expected to be as turbid as that off Surinam, the island lying only ~ 120 km NW of the Orinoco delta (van Anandel, 1967) and within the Orinoco Plume, which affects the optical properties of surface water throughout the whole SE Caribbean region (Del Castillo *et al.* 1999). With a mean freshwater outflow of $(3.10 \pm 0.38) \times 10^4 \text{ m}^3 \text{ s}^{-1}$, the Orinoco ranks as the fourth largest river in the world (Hu *et al.* 2004). The total assemblage of calcareous benthonic foraminifera from the Savonette area nevertheless comprised 8.4 % symbiont-bearing foraminifera. It might be argued that the tests of some of these symbiont-bearing species are modern and allochthonous, the disc-shaped tests of *Amphistegina* especially being susceptible to transport (Martin & Liddell, 1991). However, the dominant current in the region, the Guyana Current, flows towards the Savonette area from the southeast (Lentz, 1995). Thus, it flows from a turbid region unlikely to support a live population of *A. gibbosa* (Hofker, 1983). Furthermore, although the Guyana Current carries 20 % of the clay and silt discharged from the Amazon NE along the coast of South America as mudbanks (Meade, 1994; Eisma, Augustinus & Alexander, 1991; Eisma, 1998), such that half the sediment making up the Orinoco Delta comprises mud derived from the River Amazon (Aslan *et al.* 2003), it is unlikely that it is strong enough to transport larger foraminiferal tests also.

Poag (1981) suggested that there are five relict 'generic dominance facies' within the Gulf of Mexico: his *Elphidium*, *Elphidium–Hanzawaia*, *Bigenerina*,

Planulina and *Cibicidoides* biofacies. Although he implied that these are of Late Pleistocene age, an early Holocene age cannot be ruled out. The total benthonic foraminiferal assemblage in the Savonette area is dominated by species of *Cibicidoides* (Carr-Brown, 1972), with lesser *Elphidium* and *Hanzawaia*, and thus equates to Poag's (1981) *Cibicidoides* biofacies. Within the Gulf of Mexico the *Cibicidoides* biofacies is developed in carbonate-rich areas on the continental shelves off western Florida and around the Yucatan Peninsula. Carbonates accumulate primarily where the terrigenous input is low (Flügel, 2004). The presence of a relict *Cibicidoides* biofacies off SE Trinidad might indicate that during the early Holocene transgression, sediment was so effectively sequestered in the Orinoco delta and Amazon estuary that carbonate-producing organisms were able to move into the area. (Milliman & Meade, 1983, suggested that even at present most of the sediment carried by the Orinoco River is deposited in its upper delta.) This hypothesis is supported by Sen Gupta *et al.*'s (1991) observation that the source for clayey sediments within the Grenada basin, north of Trinidad, at the Pleistocene/Holocene boundary switched from a South American (southerly) to a Lesser Antillean (easterly) source. The reduction in turbidity engendered was sufficient to allow species with algal symbionts to establish populations off eastern Trinidad. The water need not have been extremely clear, however. *Amphistegina gibbosa*, which formed 1–15 % of the recovery of calcareous benthonic foraminifera from samples from the Savonette area, is in Florida Bay the last of the larger, symbiont-bearing foraminifera to die out as the water at a locality becomes increasingly turbid (P. Hallock, pers. comm. 2008).

The samples from the Savonette area did not present a uniformly iron-stained foraminiferal assemblage. The percentage of iron-stained planktonic foraminifera exceeded that of iron-stained benthonic ones. It has long been noted that benthonic foraminifera differ in their susceptibility to dissolution (Corliss & Honjo, 1981), *Amphistegina gibbosa* and miliolids being particularly susceptible. However, planktonic foraminifera are generally more prone to dissolution than benthonic ones (Berger, 1975). The results presented here suggest that planktonic foraminifera, in addition to being more readily dissolved, are also more disposed to staining with iron.

ANOVA (ANalysis Of Variance) showed that the percentage of iron-stained specimens differed between calcareous benthonic species, being highest in *Globocassidulina subglobosa* and lowest in *E. antillarum*. Several hypotheses may be proposed to account for this:

(1) On the basis of the elevations and ages of drowned *Acropora palmata* reefs from the Caribbean-Atlantic region, Blanchon & Shaw (1995) documented that sea-level during the early Holocene rose in at least three catastrophic, decimetre-scale events (see also Yu *et al.* 2007), synchronous with episodic collapsing of the Laurentide and Antarctic ice sheets, which

released huge volumes of subglacial and proglacial meltwater. Foraminiferal biofacies typically being arrayed by depth (Culver, 1988; Buzas, Hayek & Culver, 2007), it might be suggested that each sea-level rise induced a change in the foraminiferal community at the Savonette Field. Symbiont-bearing genera (*Amphistegina*, *Elphidium*, *Heterostegina*, *Peneroplis*) would be limited to the early stage of the transgression, when the seafloor lay within the photic zone. Should the degree of iron-staining be dependent on the time since the specimens were deposited, one might, therefore, expect these symbiont-bearing species to be more commonly stained than at least some of the remainder of the community. This was not the case; the mean percentage of the ten species forming > 5 % of the iron-stained assemblage in any one sample that had been altered was 56.8 %. Bonferroni's comparison of means, performed subsequent to the ANOVA, showed that the mean percentage abundances of stained *A. gibbosa* (61.2 %) and *E. translucens* (65.1 %) were not significantly different to the percentages of most other species in the association. Only the percentages of stained *G. subglobosa* and *H. concentrica* (71 % and 70 %, respectively) were both significantly greater than those of *A. gibbosa* and *E. translucens*, while only the percentages of *Eponides antillarum* (48 %) and *E. repandus* (28 %) were significantly lower. It might be suggested that radiocarbon dating might be used to explore this pattern further; the shallow water species should be significantly older than the deep. However, Anderson *et al.* (1997) found that on the northeastern Gulf of Mexico shelf, extensive reworking of the Holocene transgressive package has led to considerable stratigraphic disorder in foraminiferal ¹⁴C dates.

(2) Corliss & Chen (1988) attempted to distinguish epifaunal and infaunal morphotypes. It might be argued that infaunal species would be preferentially altered, being closer to the reducing zone invoked by Maiklem (1967) as harbouring sulphate-reducing bacteria and being more readily incorporated into this zone by either burial or bioturbation. However, de Stigter, Jorissen & van der Zwaan (1998) found that representatives of morphotypes at one time ascribed to an epifaunal microhabitat can live commonly in subsurface microhabitats, leading Gross (2002) to suggest that the infaunal/epifaunal dichotomy of foraminiferal microhabitats needs to be re-examined and Murray (2006) to write that 'the distinction between infaunal and epifaunal [foraminifera] is to some extent arbitrary'. Thus, no attempt can be made to discern differing staining susceptibilities on the basis of microhabitat.

(3) The three groups recognized using Bonferroni's test for equality of means may each comprise species with a similar susceptibility to staining. Murray (2006, p. 340) observed that live *Hanzawaia* occur at primarily inner neritic depths, that is, at depths comparable to *Elphidium* and *Amphistegina*. In the Savonette area, however, *H. concentrica* is significantly more stained than *E. translucens* and *A. gibbosa*. This

further suggests that the susceptibility to staining is independent of the preferred water depth at which the foraminifera live.

It has long been recognized that much of the seafloor on continental shelves worldwide is the site of relict sediment of Late Pleistocene to early Holocene age (e.g. Lyell, 1850; Stather, 1912; Shepard, 1932; Conolly & von der Borch, 1967) that was deposited during a sea-level low stand. Emery (1968) suggested that much of this relict sediment is iron-stained. Should iron-stained sediment be restricted to the transgressive systems tract, it follows that iron-stained foraminifera might prove a useful sequence stratigraphic tool. Although some of this relict sediment shows a 'palimpsest effect' (Prothero & Schwab, 1996), having been reworked so that it is in dynamic equilibrium with modern marine processes (Swift, Stanley & Curray, 1971), it will nevertheless contain some relict foraminifera specimens (Poag, 1981). Despite this incorporation of relict specimens, which at times can dominate the assemblage, total (living + dead) foraminiferal assemblages on shelves have long been accepted as being good indicators of water depth (Norton, 1930; Culver, 1988; Buzas, Hayek & Culver, 2007). This has led authors to utilize data from relict occurrences on continental shelves when proposing palaeodepths for ancient successions. For example, the New Orleans Paleocologic Committee (1966) suggested *A. gibbosa* to be an index for water 20–100 m deep, and Collins (1993) cited Drooger & Kaasschieter (1958) as her authority when using *Cassidulina norcorssi australis* and *Eponides antillarum*, respectively, to indicate shelf edge and neritic palaeodepths in the Neogene of the Bocas del Toro Basin, Panama.

Note: To counter any bias in palaeoenvironmental interpretations induced by this relict material, Murray (2006) has recommended that palaeoenvironmental inferences conducted using ecological uniformitarianism should be made using data from observations of live specimens only.

6. Conclusions

Relict sediment of early Holocene age near the continental shelf edge off SE Trinidad yields a rich assemblage of iron-stained foraminifera. Examination of this association suggests that species differ in their susceptibility to iron-staining, and that planktonic foraminifera are generally more susceptible to alteration than are benthonic ones. The fauna was dominated by *Cibicidoides* spp. A similar biofacies has been found at comparable, outer neritic depths in the Gulf of Mexico in carbonate-rich areas. This indicates that, despite the proximity of the Orinoco delta, terrigenous input to the continental shelf off SE Trinidad was much reduced early in the Holocene transgression. Of the calcareous benthonic specimens, 8.4% comprise species that are currently symbiotic with algae and restricted to the photic zone, which is at present only a few tens of

metres deep off northern South America. These species symbiotic with algae date from an interlude early in the Holocene transgression when sediment was so effectively stored within the Orinoco delta that the water on the continental shelf was rendered sufficiently clear to be inhabited by species typical of low-turbidity water.

The foraminifera have a long history of use as a tool in sequence stratigraphy (Armentrout, 1996; Orndorff & Culver, 1998; Pekar & Kominz, 2001), but few studies have placed the foraminiferal assemblages on the modern continental shelf in a sequence stratigraphic context. Should iron-stained foraminifera prove to be typical of sediment deposited during transgressions, they would prove a powerful tool for use in sequence stratigraphy.

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