Intertidal Mangrove Foraminifera From The Central Great Barrier Reef Shelf, Australia: Implications for Sea-Level Reconstruction

Sarah A. Woodroffe  
*University of Durham*

Benjamin P. Horton  
*University of Pennsylvania*, bphorton@sas.upenn.edu

Piers Larcombe  
*Centre for Environment, Fisheries and Aquaculture Science*

John E. Whittaker  
*Natural History Museum*

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Abstract

Contemporary foraminiferal samples and environmental information were collected from three fringing mangrove environments (Sandfly Creek Transect 1 and 2, and Cocoa Creek) in Cleveland Bay, and an estuarine mangrove environment (Saunders Creek) in Halifax Bay, on the central Great Barrier Reef (GBR) coastline, Australia, to elucidate the relationship of the foraminiferal assemblages with the environment. The data support the vertical zonation concept, which suggests that the distribution of foraminifera in the intertidal zone is usually a direct function of elevation, with the duration and frequency of subaerial exposure as the most important factor. An agglutinated foraminiferal assemblage dominated by *Miliammina fusca, Trochammina inflata, Ammotium directum* and *Haplophragmoides* sp. exists at the landward edge of the field sites, in a zone between just above Mean Low Water of Neap Tides to Highest Astronomical Tide level (a vertical range of 1.8 m). In addition, a foraminiferal assemblage dominated by *Ammonia aoteana* is found at all sites, existing between just below Mean Low Water of Neap Tides and Mean High Water of Neap Tides (a vertical range of 0.8 m). These assemblages may be used to reconstruct sea level from fossil cores from the area.

Comments

INTERTIDAL MANGROVE FORAMINIFERA FROM THE CENTRAL GREAT BARRIER REEF SHELF, AUSTRALIA: IMPLICATIONS FOR SEA-LEVEL RECONSTRUCTION

SARAH A. WOODROFFE1, BEN P. HORTON2, PIERS LARCOMBE3 AND JOHN E. WHITTAKER4

ABSTRACT

Contemporary foraminiferal samples and environmental information were collected from three fringing mangrove environments (Sandfly Creek Transect 1 and 2, and Cocoa Creek) in Cleveland Bay, and an estuarine mangrove environment (Saunders Creek) in Halifax Bay, on the central Great Barrier Reef (GBR) coastline, Australia, to elucidate the relationship of the foraminiferal assemblages with the environment. The data support the vertical zonation concept, which suggests that the distribution of foraminifera in the intertidal zone is usually a direct function of elevation, with the duration and frequency of subaerial exposure as the most important factor. An agglutinated foraminiferal assemblage dominated by Millammina fusca, Trochammina inflata, Ammonia directum and Haplophragmoides sp. exists at the landward edge of the field sites, in a zone between just above Mean Low Water of Neap Tides to Highest Astronomical Tide level (a vertical range of 1.8 m). In addition, a foraminiferal assemblage dominated by Ammonia nateana is found at all sites, existing between just below Mean Low Water of Neap Tides and Mean High Water of Neap Tides (a vertical range of 0.8 m). These assemblages may be used to reconstruct sea level from fossil cores from the area.

INTRODUCTION

The study of Holocene relative sea-level (RSL) changes in the Great Barrier Reef (GBR) region of Australia is particularly important because of its tectonic stability and its great distance from the centers of former ice caps. Observations of sea-level change in field locations such as Australia provide the most direct estimate of the volume of grounded ice existing at various time periods between the Last Glacial Maximum and present (Milne and others, 2002). In addition, evidence of a mid-Holocene high stand of approximately +3 m along parts of the east coast of Australia and the nature of subsequent RSL fall is of interest to geophysical modelers because it yields information on the contribution of hydro-isostasy, equatorial ocean siphoning and crustal levering to late Holocene relative sea-level change in tropical areas. This increases our understanding of solid earth geophysics (e.g., Mitrovica and Peltier, 1991; Nakada and Lambeck, 1989; Yokoyama and others, 2001; Lambeck and others, 2002).

One approach to the study of RSL change is to use microfossil sea-level indicators such as foraminifera, diatoms and pollen, which are contained in both contemporary and fossil sedimentary deposits. Sea-level indicators developed from observed changes in microfossil assemblages have been used for the past 30 years or so to provide reconstructions of Holocene RSL change for many areas, including Britain, Europe and North America, and have been the primary source of data for developing and testing models of RSL change (e.g., Shennan and others, 2002; Peltier, 2002; Shennan and Horton, 2002). Marsh foraminifera, in particular, are highly accurate sea-level indicators because they have narrow ecological tolerances and narrow vertical zones in the intertidal zone (Scott and Medioli, 1978, 1980a). However, all microfossil data and their associated RSL reconstructions are subject to errors, which limit the precision of determining both age and elevation, and as smaller magnitude sea-level changes are analyzed, the magnitude of errors becomes increasingly important. To address this limitation we must use the most precise indicators available, and use statistically robust quantitative techniques in reconstructions.

To this end, a new generation of microfossil-based quantitative paleoenvironmental reconstructions has been developed (e.g., Horton, 1999; Zong and Horton, 1999; Edwards and Horton, 2000; Gehrels and others, 2001; Horton and others, 2003), allowing a relatively precise reconstruction of former sea levels, using a statistically-based relationship between contemporary foraminiferal assemblages, their relationships to sea level and their fossil counterparts. This developing research field is generating high precision in RSL reconstructions (Horton and others, 2000; Edwards and Horton, 2000; Horton and Edwards, 2005; Sawai and others, 2004). In contrast to mid-latitude, temperate environments, there have been relatively few studies of intertidal foraminifera and their relationship to RSL in tropical coastal environments. The studies include Michie (northern Australia, 1987), Scott and others (Brazil, 1990), Barbosa and Suguio (Brazil, 1999), Haywood and others (New Zealand, 1999b, 2004b), Debenay and others (west coast of Africa, New Caledonia and northern Australia, 2000), Haslett (northern Australia, 2001), Debenay and others (French Guiana, 2002), Javaux and Javaux and Scott (Bermuda 1999, 2003), Horton and others (Great Barrier Reef coastline, Australia, 2003), and Horton and others (Indonesia, 2005). Furthermore, most studies concentrate on individual sites and do not investigate the potential for diversity in foraminiferal faunas over local or regional scales. The tropical environment has many different challenges for foraminiferal assemblages, including the widespread presence of bioturbators.

1 Department of Geography, University of Durham, South Road, Durham, DH1 3LE, UK. E-mail: S.A.Woodroffe@durham.ac.uk
2 Department of Earth and Environmental Science, University of Pennsylvania, Philadelphia, PA, 19104-6316. USA.
3Centre for Environment, Fisheries and Aquaculture Science, Pakefield Road, Lowestoft, Suffolk, NR33 0HT, UK.
4Micropalaeontology Research, Department of Palaeontology, The Natural History Museum, London SW7 5BD, UK.
STUDY AREAS

The shoreline of the central GBR is characterized by a series of north-facing coastal embayments (e.g., Halifax Bay, Cleveland Bay, Bowling Green Bay), which are protected from the dominant southeast trade wind by granite headlands or sand spits, but are open to northerly and north-easterly weather and the impact of occasional tropical cyclones (Belperio, 1983; Carter and others, 1993). Cleveland Bay lies immediately offshore from Townsville, Queensland, and Halifax Bay lies north of it, approximately 600 km north of the northernmost limit of the GBR (Fig. 1). The bays lie at approximately 19° S 146° 30' E. Cleveland Bay is approximately 20 km square and is landlocked around its southern and eastern margins by the mainland. Within the bay lies Magnetic Island, which is granitic and ~12 km in diameter, and rises to an altitude of 495 m. This island shields the northerly part of Cleveland Bay. The southern part of the bay is shielded by the granite headland of Cape Cleveland, which rises to an elevation of 357 m. Halifax Bay is more open, but the granite promontory of Cape Pallarenda also shields the southern half. Cleveland and Halifax Bays are relatively shallow, both reaching a maximum water depth of 15 m at their seaward edges (Carter and others, 1993). Complex water motions occur in Cleveland Bay, including the effects of refracted SE-generated swell waves, and the tidal range for both bays is generally mesotidal (~2.3 m; Carter and others, 1993; Larcombe and others, 1995). Australian Height Datum (AHD) is the local height datum used in this study. Mean Sea Level is 0.1 m above 0 m AHD. Lowest Astronomical Tide (LAT) is -1.86 m AHD, Mean High Water of Spring Tides (MHWST) is +1.21 m AHD, and Highest Astronomical Tide (HAT) is +2.15 m AHD.

COCOA CREEK, CLEVELAND BAY

Cocoa Creek is the southermost of four tidal creeks entering Cleveland Bay. The main channel meanders for 9.5 km through an extensive chenier plain close to the granite escarpment of Cape Cleveland, and extends 600 m seawards of the last chenier ridge through an extensive, well-developed mangrove fringe that is in places up to 400 m wide. The mangroves are mature and florally diverse, with trees up to 8 m in height. The mean spring tide range is 2.3 m. The transect at Cocoa Creek was taken perpendicular to the shoreline, in a series of sub-transsects which cover the range from -4.5 m AHD (-2.72 m LAT) to 1.16 m AHD (0.05 m below MHWST, Table 1). We collected data from 35 sample stations. We took samples at 10-cm elevation intervals where possible (apart from below LAT, where this was

<table>
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<th>Table 1. Environmental and elevation information for the 4 contemporary mangrove transects in Cleveland Bay and Halifax Bay.</th>
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not possible). The shallow subtidal and lower intertidal environment (−4.5 m AHD to −0.05 m AHD) is dominated by a silty substrate (−70% silt), with a low organic content (<5%), low salinity and neutral pH. The fringing *Rhizophora stylosa*-dominated floral zone starts at 0 m AHD, marked by a distinct change in grain size distributions from ~70% silt to ~90% clay, an increase in organic content to ~10%, increasing salinity (10–15%) and a drop in pH. The *Rhizophora stylosa* mangroves are mature and vegetation cover is dense. At 0.78 m AHD there is a transition to a Ceriops sp. floral zone, which is accompanied by an increase in organic content to ~19%, a further increase in salinity to ~20% and a further drop in pH. The transect stops at 1.16 m AHD against an unvegetated, sand-rich, 3-m-high chenier ridge.

**Sandfly Creek, Cleveland Bay**

Sandfly Creek is the northernmost and smallest of the four tidal estuaries in Cleveland Bay (Fig. 1). The main channel of Sandfly Creek meanders through a series of chenier ridges, and extends 800 m seaward of the final ridge through fairly mature mangroves and shallow tidal flats. The fringing mangroves extend along the coast on either side of the mouth of the creek for some distance, with large stands of *Rhizophora stylosa* and *Avicennia marina* at the mouth of the creek (Bunt and Bunt, 1999). The mean spring tidal range is 2.3 m.

**Sandfly Creek Transect 1**

This transect was taken diagonally from the creek mouth, perpendicular to the shoreline, and has 14 sample stations, which we placed strategically where there are changes in topography or vegetation. The transect covers a range from just below MLWST to MHWST (Table 1). The sedimentary environment consists of a silt-rich unvegetated tidal flat below approximately −0.3 m AHD, moving into a sparsely vegetated fringing *Avicennia marina*-dominated floral zone at approximately 0 m AHD, with an increasingly sandy substrate. Salinity is low in these two zones, whereas pH is neutral. At 0.15 m AHD, there is a transition to a densely vegetated *Rhizophora stylosa*-dominated floral zone, with between 80–90% vegetation cover. The substrate remains predominantly sandy. Salinity increases while pH decreases through this zone. At approximately 0.6 m AHD, a transition occurs to a second, more dense *Avicennia marina*-dominated floral zone. This floral zone is less dense than the *Rhizophora stylosa*-dominated zone it replaces. The substrate becomes more clay-rich, salinity continues to increase (~13%) and pH rises slightly. This zone is interrupted at 0.9 m AHD by an unvegetated, sand-rich chenier ridge, approximately 5 m wide and 2 m high. The mangrove continues behind this chenier ridge, consisting predominantly of *Aegiceras corniculatum* mangrove species, which are frequently inundated by saline waters from the estuarine channel.

**Sandfly Creek Transect 2**

This transect was taken perpendicular to the shoreline through a series of floral mangrove zones, approximately 100 m west of the mouth of Sandfly Creek, and has 20 sample stations, which we placed strategically where there were marked changes in topography or vegetation. The transect covers a range from just below MLWST to MHWST (Table 1). There is an unvegetated, silty tidal flat at approximately −0.8 m AHD, grading into a sparsely vegetated fringing *Avicennia marina*-dominated floral zone at −0.6 m AHD. A few small, sandy tidal channels occur in this zone. Salinity is low in these zones (~8%) and pH is relatively high. At −0.3 m AHD, there is a transition to a poorly developed *Rhizophora stylosa*-dominated floral zone. The *Rhizophora stylosa* mangroves are juvenile and do not have well-developed prop roots. Salinity increases through this zone (~13%) and pH drops to near neutral. At 0 m AHD, there is a transition to an open *Avicennia marina*-dominated floral zone. Salinity increases again through this zone (~15%), and pH remains fairly neutral. This zone is interrupted at 0.25 m AHD by an unvegetated, sand-rich chenier ridge, which is also present at Transect 1.

**Saunders Creek, Halifax Bay**

Approximately 50 km north of Townsville, in southern Halifax Bay, is Saunders Creek, which meanders through dense, estuarine mangroves towards the final shoreline, formed by a beach ridge. The transect at Saunders Creek was taken perpendicular to the estuarine channel, with a total of 10 sample stations, which we placed strategically where there were marked changes in topography or vegetation. The transect covers a range from just above MLWST to just below Highest Astronomical Tide (HAT; Table 1). The unvegetated channel is at approximately −0.5 m AHD, and has a very high sand percentage (95%), very low salinity (<5%) and relatively low pH. At −0.4 m AHD, there is a transition to a densely vegetated *Rhizophora stylosa*-dominated floral zone, with increasing salinity values (~10%), a silt-rich substrate (44% silt) and increasing pH levels. Vegetation cover is approximately 95% in this zone. At 1.4 m AHD, there is a transition to a narrow *Avicennia marina*-dominated floral zone, which has high salinity (~18%) and high pH. At 1.55 m AHD, there is a transition to an open, *Aegiceras corniculatum*-dominated floral zone. Salinity continues to increase to approximately 20%, whereas pH remains high. The substrate is silt-rich, and the density of vegetation cover decreases to approximately 60%. At 1.6 m AHD, there is a transition from an *Aegiceras corniculatum*-dominated floral zone to a salt pan. Salinity increases to approximately 28%, and vegetation cover decreases to approximately 10% and is made up of small stands of *Salicornia australis* and other salt-tolerant marsh species.

**MATERIALS AND METHODS**

We collected foraminifer samples (10 cm² surface sample by 1 cm thick) and environmental samples (30 cm² surface sample by 1 cm thick) from transects which crossed the whole of the mangrove zonation and intertidal zone where possible (following Horton, 1999). All readings were taken at low tide during a neap tidal cycle in the southern hemisphere winter. The environmental samples were analyzed for grain size, loss on ignition, pH and salinity. Salinity and pH analyses were performed by adding 25 ml of distilled water.
to 5 g of sediment and measuring levels in the water. Surface samples were generally concentrated within subenvironments near to mean sea level, particularly within the mangrove swamp, intertidal mudflat and shallow subtidal mudflat. All stations were leveled using a level and staff. An altitude for each station in relation to Australian Height Datum was achieved by either leveling the altitude of the swash mark from the previous high tide, or leveling to the sea and using a 'timed still' water reading to relate the altitudes to the tidal curve for Townsville (following Horton and others, 2003).

**Foraminiferal Analysis**

Sample preparation followed that of Scott and others (2001). Each sample was placed in buffered ethanol with the protein stain rose Bengal to identify organisms living at the time of collection (after Murray, 1991). Samples were subdivided into eight aliquots using a wet-splitter (Scott and others, 2001), and 200 tests were counted where possible. Taxonomy (Pl. 1) follows Albiani (1968), Haig (1988), Bronnimann and Whittaker (1993), Wynn-Jones (1994), Yassini and Jones (1995), Hayward and others (1999a), Revets (2000) and Horton and others (2003). Recent advances in molecular and morphometric analysis (Hayward and others, 2004a) have allowed the distinction of different morphological types of *Anomnonia*, commonly described in the literature as *Ammonia beccarii*. In light of this work we have illustrated most morphological types described in this paper as *Anomnonia aoteana* (Pl. 1).

The foraminiferal data are expressed as a percentage of dead assemblages only (following Horton, 1999). Horton (1999) found that the dead assemblage most closely resembles fossilized assemblages found in cores. However, the issue of using live, dead or total assemblages remains a matter of contention (eg., Scott and Medioli, 1980b; Murray, 2000). The dead assemblage differs from the live assemblage through life processes and postmortem changes (Murray, 1991). It has been argued by Murray (1991, 2000) and others (Horton and Edwards, 2004 in press; Horton and others, 2005) that the live component is variable and is not transferred into subsurface environments; therefore, its inclusion would degrade the utility of the dataset. By using the dead assemblage, we are able to compare our data with that of Horton and others (2003) from the same coastline. Dead individuals contribute at least 86% of the total number of tests counted at each site.

The foraminiferal preservation was generally very good, although samples in Sandfly Creek Transect 1 often yielded less than 40 specimens. For samples from the other three transects, a total of at least 200 was reached (following Patterson and Fisherbein, 1989). We used unconstrained incremental sum-of-squares cluster analysis to detect, describe and classify patterns within the foraminiferal data from Cocoa Creek, Sandfly Creek Transect 2 and Saunders Creek. We used unconstrained cluster analysis based on unweighted Euclidean distance with foraminifera as unstandardized percentage abundances to classify contemporary samples into more-or-less homogeneous groups (clusters). Detrended Correspondence Analysis (DCA) was used to represent samples as points in multidimensional space. Only samples with counts greater than 160 individuals and species that reach 5% of the total sum were included. Cluster analysis is effective in classifying the samples according to their foraminiferal assemblage, but Detrended Correspondence Analysis gives further information about the pattern of variation within and between groups, which is important because the precise boundaries between clusters can be arbitrary. The elevation of each station within the reliable clusters was analyzed to determine a vertical zonation of each intertidal environment. Cluster analysis and DCA are illustrated for Cocoa Creek in Figure 2. Other sites are not shown, but this information is available from the authors. A repository with all foraminiferal data from this study is located at http://www.CushmanFoundation.org, with reference number JFR DR200508.

**Results**

A total of 72 dead foraminiferal species were found in samples taken from the intertidal and shallow subtidal zones. The composition of the foraminiferal assemblages and their vertical zonation are given below.

**Cocoa Creek**

There were abundant foraminifera within this transect, with counts in excess of 200 possible at all sample stations (Figs. 2, 3). The dominant species in the subtidal and intertidal mudflat were *Pararotalia venusta*, *Parrellina hispidula*, *Ammonia aoteana* and *A. tepida*. The fauna in the mudflat zone was highly diverse, with up to 30 different species recorded at each sample station. The *Rhizophora stylosa* zone marks a transition from a fully calcareous assemblage to a mixed calcareous and agglutinated assemblage, dominated by *A. aoteana*, *Rosalina* sp., *Miliammina fusca* and *Paratrochammina stoeni*. The uppermost part of the transect, in the *Ceriops* sp. zone close to MHWS, has a fully agglutinated assemblage dominated by *M. fusca*, *Trocchammina inflata* and *Haplophragmoides* sp. Cluster analysis of foraminiferal death assemblages at each sample station detects three zones (Fig. 2):

- **Zone CC 1** is an agglutinated foraminiferal zone with a low species diversity (approximately 12 species per sample). The dominant species are *Miliammina fusca*, *Trocchammina inflata*, *Ammonium directum* and *Haplophragmoides* sp. The elevation range of this zone is 0.32–1.16 m AHD (vertical range of 0.84 m).
- **Zone CC IIa** is a mixed calcareous and agglutinated foraminiferal zone with a reasonably diverse fauna (approximately 18 species found at each sample station). The dominant species are *A. aoteana*, *Rosalina* sp., *Paratrochammina stoeni* and *M. fusca*. The elevation range of this zone is 0.04–0.30 m AHD (vertical range of 0.26 m).
- **Zone CC IIb** is a fully calcareous foraminiferal zone with a highly diverse fauna (approximately 30 species found at each sample station). The dominant species are *Pararotalia venusta*, *Parrellina hispidula*, *A. aoteana* and *A. tepida*. *Pararotalia venusta* alone accounts for between 20–54% of the count at each sample station. The elevation range of this zone is –4.58–0.05 m AHD (vertical range of 4.53 m).
SANDFLY CREEK TRANSECT 1

The foraminiferal preservation in the surface sediments ranged between several hundred and 0 tests per 10 cm³ (Fig. 4). The tidal mudflat had abundant and diverse calcareous species, and counts in excess of 200 were possible. The calcareous species Mililinella lakemarquienisis, Ammonia tepida and A. aoteana were dominant. In the densely vegetated, fringing Rhizophora stylosa floral zone and the more sparsely vegetated Avicennia marina floral zone, the foraminiferal counts were extremely low (as few as 8 specimens per 10cc sample), consisting of a mixture of calcareous and agglutinated species, mostly Trochammina inflata and Cribroelphidium poeynum. Only one assemblage zone was detected and classified at this site, being a calcareous zone dominated by Ammonia aoteana (T1 II). The elevation range of this zone is −0.36−0.36 m, a vertical range of 0.61 m.

SANDFLY CREEK TRANSECT TWO

Foraminiferal preservation in this transect was good, and counts in excess of 200 were possible (Fig. 5). The dominant species in the tidal mudflat were Mililinella lakemarquienisis, Ammonia tepida and A. aoteana, together accounting for between 40 and 50% of the total foraminiferal count. Generally, the assemblage in the mudflat zone was highly diverse, with up to 30 species recorded at each sample station. The foraminiferal fauna was uniform through the fringing Avicennia marina- and Rhizophora stylosa-dominated floral zones, but showed a slight increase in Ammonia tepida at the expense of A. aoteana through the Rhizophora stylosa zone. The second Avicennia marina-dominated floral zone had fluctuating values of Ammonia aoteana and A. tepida, but retained species diversity. The uppermost transect station, situated at the base of the chenier ridge, had a unique fauna consisting primarily of Quinqueloculina suborbicularis and A. aoteana (together totalling 77% of the count at this sample station). Cluster analysis of foraminiferal death assemblages at each sample station detects two zones:

- Zone T2 Ila is dominated by calcareous species, with moderately low species diversity (approximately 15 species found at each sample station). The dominant species are Ammonia aoteana and Quinqueloculina suborbicularis, with a maximum relative abundance of 45%. The elevation range of this zone is 0.1−0.3 m AHD (vertical range of 0.2 m).
- Zone T2 Iib is a calcareous foraminifera-dominated zone, with a highly diverse fauna (approximately 25 species found at each sample station). Ammonia tepida and Mililinella lakemarquienisis are the dominant species, with a maximum relative abundance of 56%. Other notable species include A. aoteana, Triloculina oblonga and Wiesnerella auriculata. The elevation range of this zone is −0.9−0.2 m AHD (vertical range of 1.1 m).

SAUNDERS CREEK

In the tidal creek, the assemblage is dominated by Ammonia aoteana (up to 80% of the total count), with low but persistent occurrences of agglutinated species Miliammina fusca and Trochammina inflata (Fig. 6). Through the fringing Rhizophora stylosa floral zone, Ammonia aoteana decreases and agglutinated species increase rapidly. Miliammina fusca peaks through this floral zone. The ratio of agglutinated to calcareous species is 60−40 through the Rhizophora zone. Moving into the Avicennia marina-dominated floral zone, Trochammina inflata gains in relative importance, and in the Aegiceras corniculatum floral zone, Trochammina inflata is the dominant species (60% of the counts). In the upper intertidal saltpan, both Trochammina inflata and Miliammina fusca dominate. Multivariate analysis of foraminiferal death assemblages from Saunders Creek delineates two zones:

- Zone SC I has both calcareous and agglutinated species and consists of eight samples. Species diversity is fairly low (approximately 15 species per sample). The dominant species are Miliammina fusca, Trochammina inflata and Ammonia aoteana, together accounting for a maximum of 84% relative abundance. The elevation range of this zone is −0.1−1.7 m AHD.
- Zone SC IIa is dominated by calcareous species, and consists of two samples from the lower end of the transect, in the tidal creek. Species diversity is low (approximately 10 species per sample), and the dominant species is Ammonia aoteana, with a maximum relative abundance of 68%. The elevation range of this zone is −0.5−0.1 m AHD (vertical range of 0.4 m).

DISCUSSION

The four transects from Cleveland Bay and Halifax Bay each show different foraminiferal assemblages across a tropical mangrove environment (Fig. 7). Sandfly Creek Transect 1 had very high and very low counts, in excess of 200 tests per 10 cm³ in the mudflat environment, but in the fringing Rhizophora stylosa and sparsely vegetated Avicennia marina zones, counts were as low as 8 tests per 10 cm³. All of the other sites had abundant foraminifera within them. There are many controlling factors on foraminiferal abundance and type, including nutrition, dissolved oxygen conditions, pH, salinity, substrate and temperature (e.g., Murray, 1968; Alve and Nagy, 1986; Boltovskoy and others, 1991; de Rijk, 1995; Barbosa and Suguio, 1999; Debenay and others, 2002; Horton and others, 2003). Barbosa and Suguio (1999) and Horton and others (2003) show that the foraminiferal assemblages in the coastal mangroves of Brazil and the GBR coastline, respectively, are controlled by the elevation with respect to the tidal frame. However, ground temperature, sparse vegetation cover, low organic content and low nutrient availability are particularly important considerations in tropical locations, where ponded water in the intertidal zone can reach temperatures of over 40°C between tidal inundations and there is less organic food available (Murray, 1968; Dublin-Green, 1992; de Rijk, 1995).

Sandfly Creek Transect 1 was relatively acidic. The pH variations within intertidal environments are generally greater than in any other marine environment (Phleger and Bradshaw, 1966), and pH has an effect on both the protoplasmic cell and the calcareous test of foraminifera. Experiments using live Ammonia in normal salinity waters of different pH show that decalcification begins at values below 7.5 (Le
PLATE 1

Fig. 1a Acupeina triperforata (Millett) side view, ×120. Fig. 1b Acupeina triperforata (Millett) oblique apertural view, ×120. Fig. 2a Haplophragmoides sp. (L’Orbigny) side view, ×120 Fig. 3a Ammosueta salsa (Cushman & Bronniman) oblique apertural view, ×150. Fig. 3b Ammosueta salsa (Cushman & Bronniman) side view, ×150. Fig. 4a Ammotium directum (Cushman & Bronniman) side view, ×150. Fig. 4b Ammotium directum (Cushman & Bronniman) oblique apertural view, ×160. Fig. 5a Miliummina fusca (Brady) apertural view, ×176. Fig. 5b Miliummina fusca (Brady) side view, ×136. Fig. 5c Miliummina fusca (Brady) side view, ×136. Fig. 6a Trochammina inflata (Montagu) spiral
Cadre and others, 2003), and Alve and Nagy (1986) report dissolution of tests under a pH range of 6.5–7.2. Low pH is unfavorable for calcareous foraminifera, and individuals must spend considerable energy recalcifying their tests.

The low intertidal mudflat at Sandfly Creek Transect 1 had an average pH of 7, whereas the pH in the vegetated Rhizophora stylosa and Avicennia marina zones ranges from 6.2–6.6, within and below the reported pH range which may cause dissolution of tests. This may explain the total absence of calcareous foraminifera in Sandfly Creek Transect 1 through the vegetated zones, which are below the elevation range where agglutinated foraminifera are found. Levels of pH through the vegetated zones at Sandfly Creek Transect 2 remain above 7.5, so total dissolution of calcareous tests does not occur. Debenay and others (2002) argue that decomposition of leaf litter in mangrove zones by bacterial activity lowers pH and contributes to the disappearance of calcareous foraminifera. These local-scale variations in pH levels impact greatly on foraminiferal presence and abundance.

Multivariate analysis of samples from Sandfly Creek Transect 2, Cocoa Creek and Saunders Creek shows a series of foraminiferal assemblages which cluster in relation to elevation. However, none of the transects cover the whole intertidal zone from LAT to HAT because of morphological constraints such as chenier ridges (Fig. 7). This is reflected in the foraminiferal assemblage zones found at each location.

Agglutinated species Miliammina fusa, Trochammina inflata, Ammonia aoteana, Ammotium directum and Haplophragmoides sp. dominate zones CC I and SC I, along with persistent occurrences of Ammonia aoteana at Saunders Creek only.
These zones are found towards the landward edge of the mangrove study sites at Cocoa Creek and Saunders Creek, in the elevation range -0.1-1.7 m AHD (range 1.8 m, just above MLWNT to close to HAT). Similar faunal assemblages have been found in other tropical locations. Horton and others (2003) identify two faunal zones dominated by agglutinated foraminifera at the landward edge of a separate transect at Cocoa Creek, Cleveland Bay, Australia. In Indonesia, Horton and others (2005) also identify an agglutinated upper mangrove assemblage with *Trochammina inflata* and *Miliammina fusca* on islands off southeastern Sul-
wesia, and furthermore, Debenay and others (2000) have identified agglutinated foraminifera (Jadammina macrescens and Trochammina inflata) in upper marshes in New Caledonia and Cairns, northeastern Queensland, Australia.

Zones CC IIa, T1 II, T2 IIa and SC IIa at Cocoa, Sandfly and Saunders creeks have assemblages with low species diversity and dominated by Ammonia aoteana, accounting for 20–68% of the total count at each sample station in each zone. The elevation range is –0.5–0.3 m AHD (range 0.8 m, just below MLWNT to just below MHWNT). Other studies from tropical and subtropical locations have shown an Ammonia-dominated assemblage in the mid-intertidal zone (e.g., Haslett, 2001, in the upper part of the tidal flat at the Barron River estuary, Cairns, northeastern Queensland, Australia; Hayward and others, 1999, in tidal flats and mangrove forests in New Zealand; and Horton and others, 2005, in Indonesia). It is also found in a lower estuarine environment in Brazil (Barbosa and Suguio, 1999).

Faunal zones CC IIb and T2 IIb are found at the seaward edge of transects at Cocoa and Sandfly Creeks. They have diverse calcareous assemblages dominated by Pararotalia venusta, Ammonia tepida and Pararotalina hispidula, and an elevation range of –4.58–0.20 m AHD (range 4.78 m, –2.72 m LAT to just above MTL). Haslett (2001) found a diverse foraminiferal assemblage, dominated by A. beccarii but with many other shallow marine benthic and planktonic species, in the lower intertidal zone of the Barron River estuary, and Horton and others (2003) observe a similar calcareous dominated assemblage at Cocoa Creek in the intertidal mudflats. This study is one of the first in tropical Australia to extend the sampling of intertidal mudflats to below the limit of LAT, into the shallow subtidal area. It shows the extension of this diverse calcareous zone beneath the intertidal zone and implies that for this low intertidal/shallow subtidal assemblage, the duration and frequency of tidal inundation may not be the most important limiting factor.

No clear link between foraminiferal assemblages and floral zones can be established from our new field sites. The Ammonia aoteana-dominated zone is correlated with an upper mangrove, Avicennia marina-dominated floral assemblage at Sandfly Creek, a fringing Rhizophora stylosa zone at Cocoa Creek, and with a vegetation-free creek bed at Saunders Creek. Sandfly Creek Transect 2 shows a transition from mudflat to Rhizophora stylosa-dominated floral assemblage at a lower elevation than at the other two sites. This may explain why the Ammonia aoteana zone at Sandfly Creek is higher in the mangrove sequence than at the other two sites, despite being at a similar elevation. Localized differences in mangrove zonation may be determined on a small scale by factors such as sediment transport and nutrient availability, as well as by tidal inundation frequency (Bunt and Bunt, 1999). Floral zones appear to respond to the local environment, while foraminiferal zonation occurs at similar elevations at different types of sites.

**Implications for Sea-Level Studies**

Past foraminiferal studies in temperate environments (e.g., Scott and Medioli, 1978; Jennings and Nelson, 1992; Horton, 1999; Gehrels and others, 2001) have indicated that a vertical zonation of foraminifera occurs in the intertidal zone, where the distribution of foraminifera is a direct function of elevation, with the duration and frequency of intertidal exposure as the most important environmental factors. Scott and others (2001) state that a vertical zonation of marsh foraminiferal assemblages exists on a worldwide scale, and suggest that the same 8–10 species of marsh foraminifera are ubiquitous worldwide in the upper part of the intertidal zone. Information on vertical zonation trends in tropical environments are more limited, and the evidence which exists points to a range of environmental factors being important. In New Zealand, salinity and elevation are shown as jointly the most important factors governing foraminiferal distribution (Hayward, 1999a, 1999b; 2004b), and Debenay and others (2000) show that in mangroves a range of environmental factors are important, including salinity and the presence or absence of vegetation.

An important issue when considering the applicability of foraminiferal zones in sea-level reconstructions is the preservation of foraminifera in fossil deposits. Agglutinated foraminifera within high-marsh environments have been used to precisely reconstruct former sea levels in temperate salt marshes (e.g., Gehrels, 2000; Gehrels and others, 2002; Horton and others, 2005). Many fossil cores have been collected from tropical mangrove and estuarine environments on the Great Barrier Reef coastline. These deposits have many calcareous benthic foraminifera preserved within organic-rich horizons, but no foraminifera are preserved within organic-rich horizons (e.g., Fig. 8). The organic horizons have grain size characteristics and organic content similar to those of modern mangrove environments, and preserve abundant mangrove pollen. Taphonomic loss of foraminiferal tests due to post-mortem disaggregation is an important obstacle in the use of mangroves (mainly agglutinated) foraminifera in palaeoenvironmental reconstructions in this location. The low pH environment of mangroves is not favorable for the preservation of calcareous foraminifera; however, agglutinated
Foraminifera are also not readily preserved in mangrove horizons. Studies show that thin-shelled tests such as those of *Miliammina obliqua* rapidly dis aggregate on burial (Hayward and others, 2004) and even handling of materials in the field and laboratory may affect test preservation (Wang and Chappell, 2001). We do not find even the most robust agglutinated species (e.g., *Trochammina inflata*) preserved in cores. Because of the absence of upper intertidal agglutinated foraminifera in fossil deposits from the Great Barrier Reef coastline, it is important for us to understand contemporary vertical zonation trends within mid- to low-intertidal calcareous faunas which live in muddy environments. These may be used, albeit with potentially decreased precision, to allow quantitative sea-level reconstructions using foraminiferal assemblages from this area.

An assemblage made up solely of calcareous species, but which exists only between MLWNT and MHWNT (range of 0.7 m) and is dominated by *Ammonia aoteana* may be a useful sea-level indicator in this environment because of the problems associated with removal of agglutinated foraminifera from fossil sediments. This assemblage often exists below the limit of fringing mangroves, and therefore is unlikely to be affected by large pH excursions experienced in vegetated zones. However, in some locations where mangroves extend lower into the intertidal zone (e.g., Sandfly Creek Transect I), low pH within the mangrove will likely cause the dissolution of calcareous tests such as those of *A. aoteana*.

Where agglutinated foraminifera are preserved in fossil deposits, a modern agglutinated assemblage which exists between MLWNT and HAT (range 1.8 m), consisting primarily of *Miliammina fusca*, *Trochammina inflata*, *Ammonium directum* and *Haplophragmoides* sp. may be the most useful sea-level indicator, depending on the degree of preservation of calcareous foraminifera in the fossil cores. The usefulness of different modern foraminiferal assemblages in reconstructing sea levels should, therefore, be assessed on a core by core basis.

In the tropical mangrove environments studied, local scale factors affect foraminiferal distributions. Limitations to using foraminifera as precise indicators in sea-level reconstructions include low pH excursions causing dissolution of calcareous tests and the potential problem of taphonomic loss of agglutinated foraminifera in fossil deposits.

**CONCLUSIONS**

Statistical analysis of the foraminiferal death assemblages from all sites supports numerous studies from temperate and tropical regions that indicate a vertical zonation of foraminifera exists within the intertidal zone. An upper mangrove foraminiferal zone dominated by agglutinated species, including *Trochammina inflata*, *Paratrochammina stoeni* and *Miliammina fusca*, exists in the higher tidal elevation range (−0.1–1.7 m AHD) at Cocoa Creek and Saunders Creek. A mid-intertidal foraminiferal zone dominated by *Ammonia aoteana* (−0.5–0.3 m AHD) exists at all sites. A low intertidal foraminiferal zone, dominated by *A. aoteana*, *A. tepida* and numerous other calcareous species (−4.58–0.2 m AHD), exists at Cocoa Creek and Sandfly Creek. The only
foraminiferal zone present at all locations is an A. aoteana-dominated foraminiferal assemblage between -0.5+0.3 m AHD (just above MLWNT to MHWNT).

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