ZOOXANTHELLATE SCLERACTINIAN CORALS OF THE BOWDEN SHELL BED, SOUTHEAST JAMAICA

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The zooxanthellate coral fauna of the Bowden shell bed in southeast Jamaica consists of 38 species, and is dominated by extinct free-living species belonging to the genera *Manicina*, *Thysanus*, *Trachyphyllia*, *Placocyathus* and *Antillia*. Eighteen of the species are free-living, eleven are massive and nine are branching. Only nine of the 38 species are extant, and all but one species are distributed throughout the Caribbean region. Assuming a geologic age of 3.8-2.7 Ma for the Bowden shell bed, eight of the 38 species have global last occurrences in the Bowden Formation, and eight have global first occurrences either in the Bowden Formation or in units of equivalent age elsewhere in the Caribbean.

Recent collections made at closely spaced intervals through the Bowden-Old Pera sequence reveal a shift between ~3.3-1.8 Ma from extinct free-living species to extant branching and massive species. The Old Pera collections contain a mixture of Caribbean coral species that dominated Caribbean reefs before or after an episode of accelerated faunal turnover between 4-1 Ma, and thus represent a transitional fauna. Most notable among the Old Pera species is the co-occurrence of now extinct *Stylophora granulata* and extant *Acropora cervicornis*. New stratigraphic data reveal that 18 of the 37 Old Pera species have global last occurrences in the Old Pera beds or in units of equivalent age elsewhere in the Caribbean, suggesting that it may have provided a refuge for pre-turnover species.

Comparisons with collections of two similar-aged faunas on the north coast of Jamaica, the Manchioneal Formation (2-1.4 Ma) and Hope Gate Formation (1.8-1 Ma), show striking differences that appear related to environmental conditions. The north coast faunas contain high percentages of extant species with massive colony shapes, indicative of exposed, open reef environments. Community change associated with Plio-Pleistocene turnover may have proceeded more slowly in protected, reef margin environments, such as the Old Pera beds.

Key words — Pliocene, Jamaica, Bowden shell bed, Old Pera beds, Manchioneal Formation, Hope Gate Formation, scleractinians, reefs, extinctions, chronostratigraphy.

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INTRODUCTION

The Bowden shell bed has long been known for the abundance and exceptional preservation of extinct, free-living, flabelloid reef corals that are typically associated with sea grass flats (Vaughan, 1919; Robinson, 1969; Budd *et al.*, 1996; J.W. Wells, pers. comm., 1988). It is also the type

locality for at least ten named Mio-Pliocene reef coral species. Duncan (1863) designated holotypes for five species from specimens collected in the Bowden shell bed such as *Placocyathus barretti*, *Placotrochus alveolus* (= *Placocyathus*), *Thysanus excentricus*, *Siderastrea grandis* (= *S. siderea*) and *Cyphastrea costata* (= *Solenastrea bournoni*). In Duncan & Wall (1865), he designated holotypes for four more species, viz. *Placocyathus moorei* (= *P. barretti*), *Thysanus elegans* (? = *T. excentricus*), *Stylophora granulata* and *Antillia walli* (= *Trachyphyllia bilobata*). Vaughan (1901) also based the new species, *Antillia gregorii*, on a specimen from the Bowden shell bed which Duncan (1863) originally identified as '*Montlivaltia ponderosa* Edwards & Haime'.

Despite its importance to taxonomy, the Bowden fauna is poorly known. The last complete published description was that of Vaughan (1919), who listed 13 zooxanthellate coral species and commented on similarities with what is now known as the Mio-Pliocene Gurabo Formation of the northern Dominican Republic and the early Pliocene Pinecrest Beds of south Florida. However, Aubry (1993) dated the Bowden shell bed as early late Pliocene or 3.8-2.7 Ma (Aubry, 1993), and thus younger than the Gurabo Formation and possibly also younger than the Pinecrest reef coral horizons. Therefore, it may represent one of the youngest predominantly 'pre-turnover' faunas in the Caribbean, before accelerated origination and extinction transformed the species composition of Caribbean reefs during late Pliocene and early Pleistocene time (Budd *et al.*, 1994; Johnson *et al.*, 1995; Budd *et al.*, 1996; Budd & Johnson, 1997).
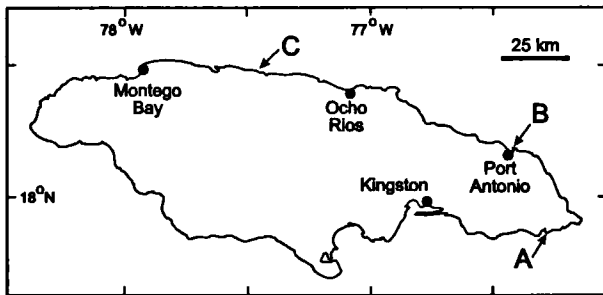

Fig. 1. Outline map of Jamaica showing the general locations of the three reef coral faunas considered herein; A — the Bowden-Old Pera sequence along the coast of Port Morant Bay, parish of St Thomas; B — the Manchioneal Formation at Folly Point and Navy Island near Port Antonio, parish of Portland; and C — the Hope Gate Formation in the Rio Bueno area, parish of Trelawny.

The purpose of this contribution is to present a new, up-to-date description of the fauna based on our 1994 collections of reef corals from the Bowden shell bed, and through the Bowden-Old Pera sequence along the east coast of Port Morant Bay (Figs 1, 2). The stratigraphy of

the Bowden-Old Pera sequence is also newly revised using palaeomagnetic data. We compare the taxa identified in these collections with other Jamaican collections that we made in 1994 through coastal sequences of similar geologic age within the Manchioneal Formation on Navy Island and Folly Point near Port Antonio (northeastern Jamaica), and within the Hope Gate Formation near Rio Bueno and Discovery Bay (north-central Jamaica) (Fig. 1). We then use museum collections of the Bowden shell bed to assemble a complete faunal list and re-evaluate the evolutionary significance of the Bowden reef coral fauna.
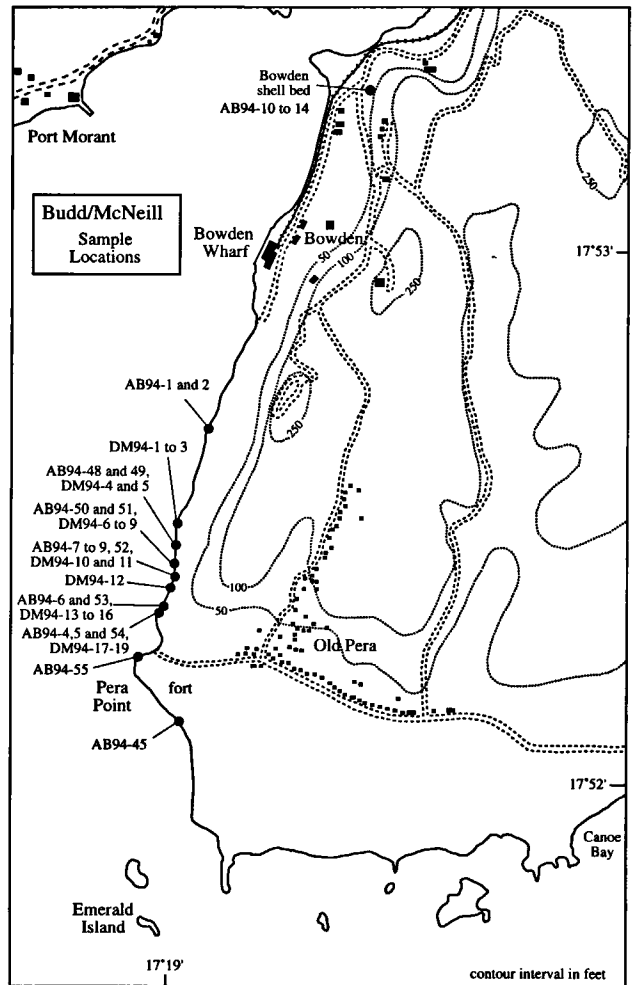
Fig. 2. Map showing the locations of stratigraphy (DM series) and coral (AB series) sample sites in the Bowden-Old Pera sequence along the coast of Port Morant Bay.

THE BOWDEN-OLD PERA SEQUENCE ALONG THE COAST OF PORT MORANT BAY

Existing stratigraphy of the Bowden shell bed — Several recent stratigraphic studies on the Bowden Formation have provided new information on the age of the classical Bowden shell bed and adjacent lithologic units.
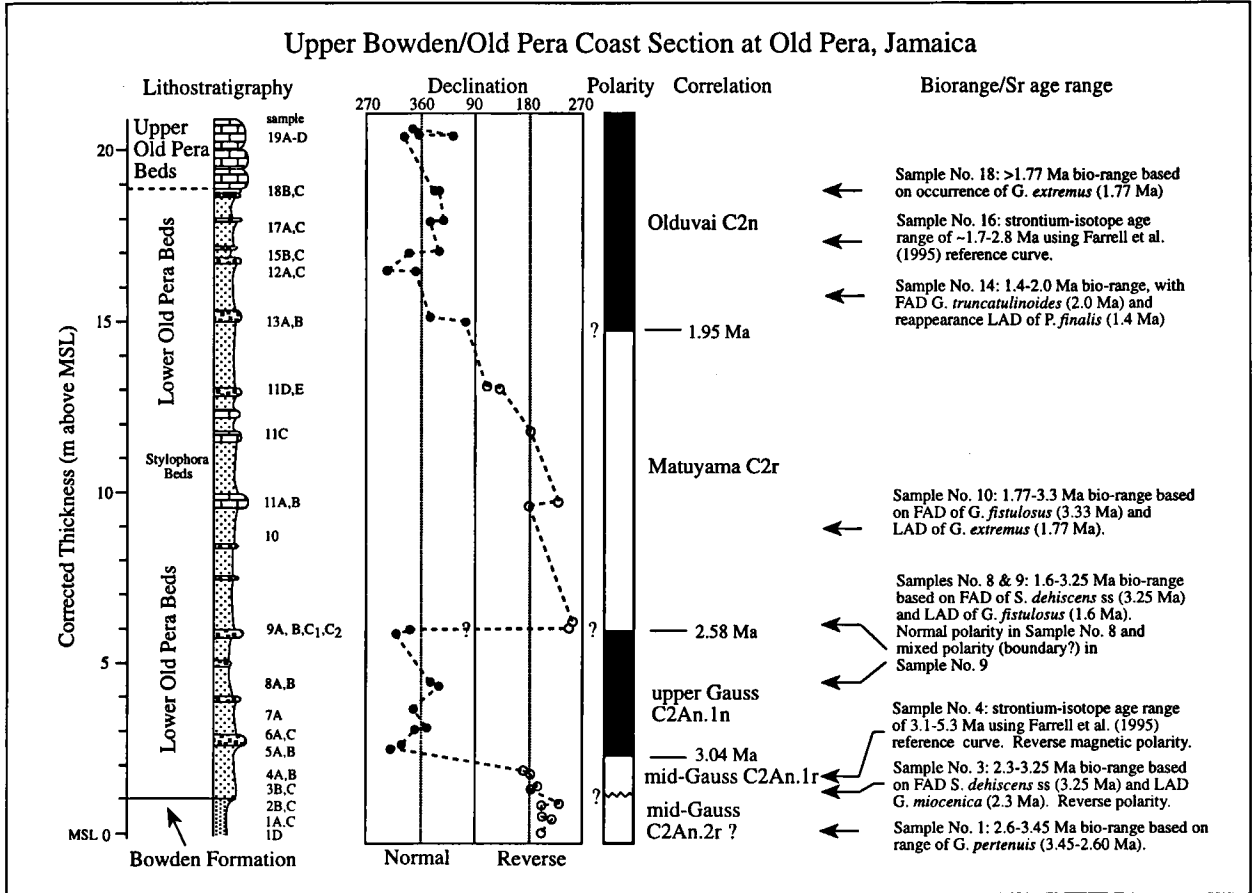
Fig. 3. Biostratigraphic, palaeomagnetic and strontium isotope data collected in the Bowden-Old Pera sequence.

Banner & Blow (1965), in their construction of a planktonic foraminiferal biostratigraphy of the Neogene, examined samples from the Bowden shell bed and, based on their zonation at that time, assigned them to zone N19 (Pliocene). Robinson (1969) cited a personal communication with W.H. Blow as a revision of the Bowden shell bed to at least the boundary between zone N19 and the newly established zone N20, if not entirely in zone N20. Robinson (1969) also indicated that the upper part of the type section, along the coast near the town of Bowden, may extend into younger zones.

A combination of planktonic foraminiferal biostratigraphy and palaeomagnetic data on the Bowden type section was presented by Robinson & Lamb (1970). Two sample sites, one near the Bowden shell bed (ER1146 = AB94-10 to 14) and one upsection near the Bowden type section (ER1123 = DM94-1 to 3), had normal and transitional polarity, respectively (Fig. 2). Combined with the biostratigraphy, these palaeomagnetic data led to an upper Gauss chron (C2An.1n) correlation, that is, late Pliocene.

More recent biostratigraphic re-examination of correlative sections of the Bowden Formation (Aubry, 1993; Berggren, 1993) have confirmed a Pliocene age. Calcareous nannofossil stratigraphy of the sections has shown a zone NN16 assignment for most of the exposed part of the Bowden Formation, and a zone NN15 assignment for its lower beds (Aubry, 1993). The Bowden Formation type section and nearby road to Arcadia section was assigned to zone NN16. Planktonic foraminifera examined by Berggren (1993) at the same correlative sections were assigned to zones PL2 to PL3, which spans the early/late Pliocene boundary between the Gilbert (C2Ar) chron and the Gauss (C2An.3n and C2An.2) chron. These foraminiferal zones are consistent with the age range that comprises the above mentioned nannofossil zonal assignment of NN16 and part of NN15.

New stratigraphic data and provisional interpretation — We developed a provisional stratigraphy for the upper part of the Bowden Formation type section and the overlying Old Pera beds based on a combination of planktonic foraminiferal biostratigraphy, strontium-isotope stratigraphy and magnetostratigraphy (Figs 3, 4). A total of 19 sites were sampled along the coast south of the town of Bowden (Fig. 2). Palaeomagnetic samples were collected at 17 stratigraphic levels within the approximately 20 m section and multiple samples were analysed at each level. Microfossil samples were collected at all 19 sites, and strontium-isotope samples were collected at DM94-4, DM94-16 and in the Bowden shell bed.
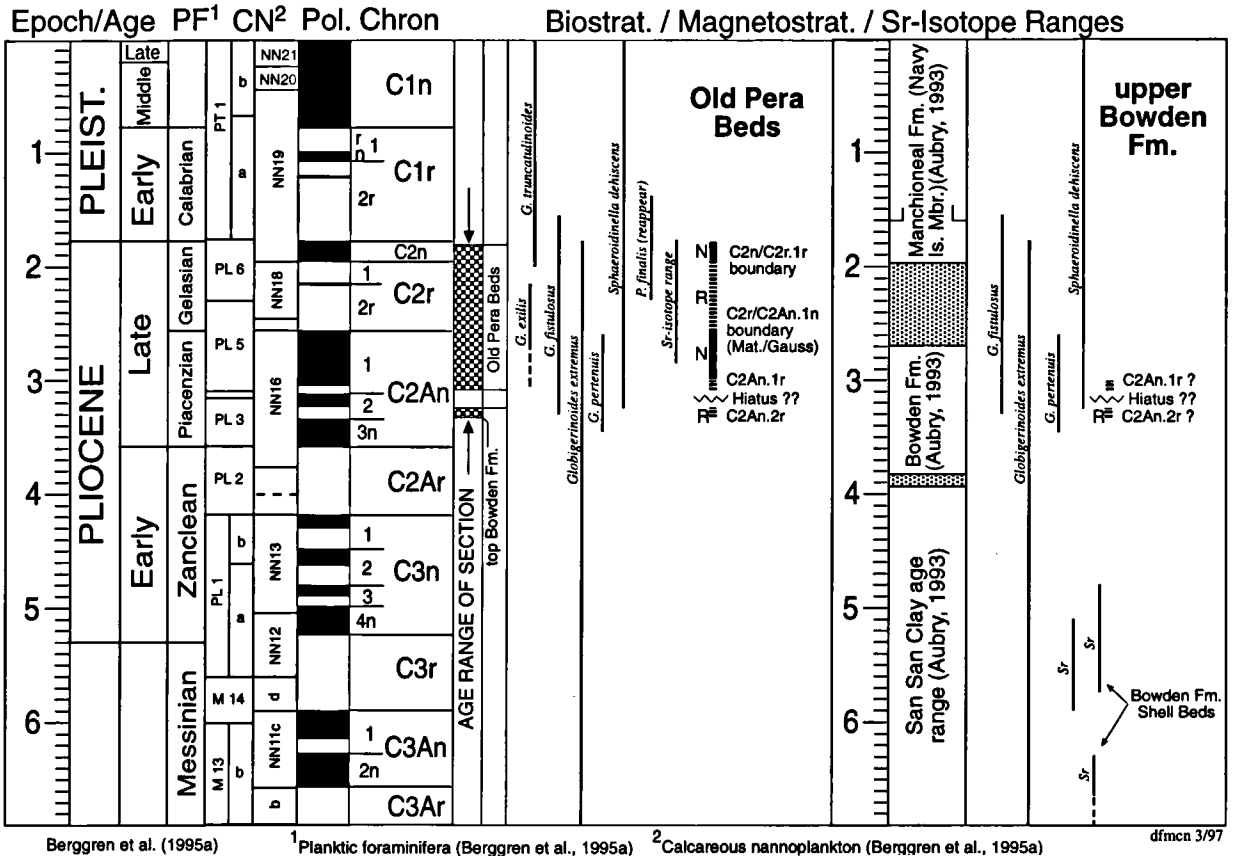
Fig. 4. Chronostratigraphic summary for the Bowden-Old Pera sequence.

Palaeomagnetic samples were collected using a field drill and oriented using a Brunton compass. They were analysed in a shielded room using a 2G-755 superconducting magnetometer at the University of Miami, and demagnetised using alternating field and thermal demagnetisation techniques. Unweathered silty/clay sands from the Bowden Formation had a very stable component of magnetic remanence with only a very soft viscous overprint which was removed in the first few alternating field demagnetisation steps.

Selected rock-magnetic tests and thermal demagnetisation character suggested a magnetite mineralogy as a carrier of magnetic remanence. Limestones from the Old Pera beds were weaker than the Bowden Formation samples, but were also very stable during demagnetisation. Similar to many Tertiary limestones, the Old Pera samples became weak and unstable by thermal steps at about 400° to 450°. The unaltered nature of the Bowden Formation samples, the characteristic response of the limestones to demagnetisation, and the stable, linear decay of the remanence are interpreted here to represent a primary component of magnetisation. The palaeomagnetic results were interpreted using the geomagnetic polarity timescale of Berggren et al. (1995a).

Strontium-isotope samples were measured at the Uni-

versity of Florida and ages assigned using the standard reference curve of Farrell et al. (1995). Sample mineralogy was determined by X-ray diffraction, and stable-isotope values were measured to assure original mineralogy and detect potential secondary, meteoric alteration.

A total of four geomagnetic polarity zones were recognised; two normal and two reverse polarity (Fig. 3). The top of the Bowden Formation had a reverse polarity which continued into the lower Old Pera beds. A 4 m normal polarity section occurs over the Bowden Formation which in turn is overlain by about 9 m interval of reverse polarity. This reverse polarity zone is sampled at only four levels due to poor outcrop conditions which prevented in situ sampling. The upper 5-6 m of section, where the more massive limestone beds of the upper Old Pera beds occur, had a normal polarity (Fig. 3).

Diagnostic biostratigraphic markers and several strontium-isotope ages allow a correlation of the polarity reversal sequence to the geomagnetic polarity time scale. The uppermost portion of the Bowden Formation sampled in our section has several age diagnostic planktonic foraminifera which constrain a late Pliocene age (Fig. 3). For example, the occurrence of Globorotalia pertenuis and Sphaeroidinella dehiscens sensu stricto have first appearances at 3.45 Ma and 3.25 Ma, respectively (Berggren et

al., 1995a). These first appearances suggest a mid-Gauss chron (C2An.2) or younger age for the upper Bowden Formation. A strontium-isotope age range (3.1-5.3 Ma) on a sample about 1 m above the top of the Bowden Formation suggests an age constrained between 3.25 to about 3.0 Ma. Reverse polarity within this age range would correlate to either C2An.1r (3.04-3.11 Ma) or C2An.2r (3.22-3.33 Ma). We are unable to determine whether a hiatus is present between the top of the Bowden Formation and the lower part of the Old Pera beds. If no hiatus is present the reverse polarity could be correlated to the younger of the two choices (C2An.1r), and if a gap occurs it could be sub-chronozone C2An.2r.

The overlying normal polarity zone is correlated to the upper part of the Gauss chron (C2An.1n, 2.58-3.04 Ma). This correlation is based on the co-occurrence of *S. dehiscens s.str.* (FAD 3.25 Ma) and *Globigerinoides fistulosus* (3.33-1.6 Ma) as well as *Globigerinoides extremus* (LAD 1.77 Ma) in this interval and above (sample DM94-10). The overlying reverse polarity is correlated to the Matuyama chron C2r, although only one sample yielded good biostratigraphy (Fig. 3). This correlation is based on the co-occurrence in sample DM94-10 of *G. fistulosus* (3.33-166 Ma) and *G. extremus* which has a last appearance at 1.77 Ma. This LAD of *G. extremus* coupled with reverse polarity would suggest a Matuyama chron C2r correlation. The overlying normal polarity which caps the section has several good biostratigraphic constraints which would suggest a correlation to the Olduvai subchron C2n (1.77-1.95 Ma). Sample DM94-14 marked the first occurrence of *Globorotalia truncatulinoides*, which in the Atlantic indicates a 2.0 Ma age or younger (Berggren *et al.*, 1995a). This correlation is also consistent with a strontium-isotope age range measured from an aragonite shell at the level of sample 16. Last, *G. extremus* (LAD 1.77 Ma) is still present in the stratigraphically highest sample that yield planktonic foraminifers. The massive, upper Old Pera beds had normal polarity and, although no biostratigraphy is available, are thought to also be part of the Olduvai subchron.

In summary, the age of the uppermost Bowden Formation at its type section and the overlying Old Pera beds is interpreted here to be late Pliocene (Fig. 4). This age is consistent with age estimates from several existing biostratigraphic studies. The age of the upper portion of the Old Pera beds has the potential to be similar age with the Manchioneal Formation on the northeast coast (Robinson, 1969) based on the occurrence of *G. truncatulinoides*, although data from Kohl (1992) suggest a slightly younger age of earliest Pleistocene age. These may also be age equivalent (latest Pliocene to earliest Pleistocene) to the Hope Gate Formation on the north-central coast (Land, 1991) based on initial strontium-isotope age constraints.

It is interesting to note, however, that strontium-isotope age ranges on three shell samples from the classic Bowden shell bed (see location on Fig. 2) all yielded ages older than 5 Ma (Fig. 4). Since this Bowden shell bed location is not directly tied to the stratigraphy of the section we examined, three explanations can be proposed. First, the Bowden shell bed unit is stratigraphically below the base of our section which sampled the uppermost part of the Bowden Formation. This is very likely since the Bowden shell bed site is to the north of our section and dips are southerly and southwesterly which would put the shell beds below our lowermost sample. In addition, Robinson & Lamb (1970) measured normal polarity at the shell bed site while we measured reverse polarity in the upper part of the Bowden Formation. The late Miocene strontium-isotope age ranges would put the shells equivalent to the age of the San San Clay (Aubry, 1993). The two other explanations for the apparently older-than-expected ages would be that the shells are reworked or that they have precipitated or have been altered in less radiogenic fluids. The potential for reworking does exist since the depositional setting for the Bowden Formation sediments is a deeper water slope (>100 m water depth), and it does contain intervals of al-lochthonous material introduced from shallow water by gravity mechanisms (Robinson, 1969). Since there are only three strontium-isotope analyses at this time no definitive answer can be reached. Clearly, additional detailed strati-graphic and geochemical analyses are needed to resolve this uncertainty.

Coral assemblages — During June 1994, we made collec-tions of zooxanthellate scleractinian corals along the east coast of Port Morant Bay at seven sites in the Bowden Formation and 15 sites in the Old Pera Beds of the overly-ing Manchioneal Formation (Fig. 2; Table 1). Each site was approximately 2-3 m high and 10-15 m wide. At each site, specimens representative of the species composition were individually extracted from the outcrop with a rock hammer. A total of 138 specimens were collected in the Bowden Formation and 156 specimens in the Old Pera beds. All the collected specimens were shipped to Iowa, prepared, identified, and entered into a specimen database available on the World-Wide Web at http://porites. geol-ogy.uiowa.edu. The material will be deposited at the United States National Museum of Natural History (USNM), the Florida Museum of Natural History (UF), and the Paleontology Repository of the University of Iowa (SUI); other figured specimens are from the Geology Mu-seum, University of the West Indies, Mona (UWIGM).

Specimens were identified to species using a consistent set of characters and states developed from morphometric analyses of Neogene and Recent samples collected across the Caribbean region (see Budd *et al.*, 1994; Budd & John-son, 1997). Lists and illustrated definitions of these char-acters together with information on species authorship and synonyms are also currently available on the World-Wide Web at the above address. A total of 24 species (6 extant; 25%) were identified in the Bowden Formation collections, and 37 species (14 extant; 37.8%) in the Old Pera beds collections (Table 2; Pls 1, 2).

Of the 24 species identified in the Bowden Formation

collections, 16 (66.7%) are free-living, and most of these free-living species belong to the genera *Manicina* (Pl. 1g-j) and *Thysanus* (Pl. 1k-n) in the family Faviidae (see Budd & Johnson, 1998; Johnson, 1998), and to *Placocyathus* (? = *Meandrina*) in the family Meandrinidae (Pl. 2c-f). *Placocyathus alveolus* (Duncan, 1863) and *Thysanus excentricus* Duncan, 1863 are by far the most abundant species in the collections. The free-living coral *Trachyphyllia bilobata* (Duncan, 1863) (Pl. 2b) is also very common. Five species are branching, the most abundant of which are *Stylophora monticulosa* Vaughn *in* Vaughn & Hoffmeister, 1925 (Pl. 1c) and a new, unnamed species of *Acropora*, herein called '*Acropora* sp. Z' (Pl. 1d). Massive corals are less common, and consist of two environmentally tolerant extant species, *Solenastrea bournoni* Milne Edwards & Haime, 1849 (Pl. 2a) and *Porites astreoides* Lamarck, 1816 (Pl. 1e). The exceptionally high number of free-living corals in the Bowden shell bed suggests that they were living in a protected, muddy environment, perhaps associated with sea grass flats (Budd *et al.*, 1996).

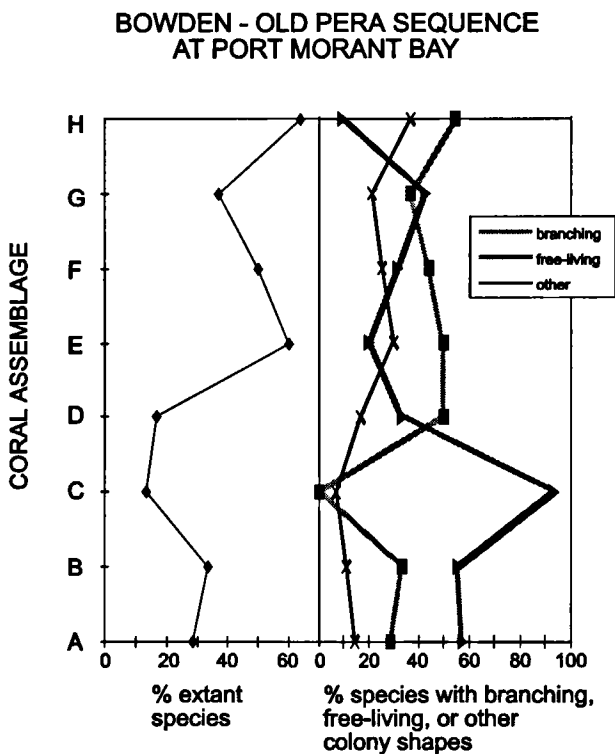**BOWDEN - OLD PERA SEQUENCE AT PORT MORANT BAY**

Fig. 5. Percentages of extant species, and species with branching, free-living, and other (massive and platy) colony shapes in eight coral assemblages in the Bowden-Old Pera sequence at Port Morant Bay. The localities included are listed in Table 1.

In contrast, the Old Pera beds collections contain 12 free-living (32.4%), 13 branching (35.1%), and 11 massive species (29.7%). The most abundant taxa are the Recent species *Acropora cervicornis* and the Neogene species *Stylophora granulata*. The co-occurrence of these two spe-

cies is especially significant, because *S. granulata* dominated Caribbean mid-forereef zones during the Neogene prior to turnover and *A. cervicornis* has dominated them since the Plio-Pleistocene (Budd & Johnson, 1997). The Old Pera beds thus contain a transitional fauna in which members of pre- and post-turnover communities lived side-by-side. In this respect, they resemble early late Pliocene faunas in the Limon Group of Costa Rica (Buenos Aires trend) (Budd *et al.*, 1998), but not Plio-Pleistocene portions of the Bahamas Drilling Project cores (Budd & Kievman, 1993), where members of the old and new fauna do not co-occur.

To examine patterns of faunal change upsection, the 22 collecting sites were grouped into eight coral assemblages (Table 1), and trends in percentages of extant species and species with branching, free-living, massive, and platy colony shapes were qualitatively examined upsection (Fig. 5). The patterns suggest a shift from predominantly free-living to branching shapes at the Bowden-Old Pera boundary (that is, between assemblages C and D), although beds with abundant free-living corals occasionally occur within the Old Pera beds (such as assemblage G). Non-parametric statistical tests (Mann-Whitney U) indicate that the Bowden Formation contains significantly more free-living species ($Z = -2.236$, $p = .0253$) and fewer branching ($Z = -2.249$, $p = .0245$) and massive or platy ($Z = -2.236$, $p = .0253$) species than the Old Pera beds. Despite this shift, the lowest Old Pera assemblage (assemblage D) contains a low percentage of extant coral species, similar to the Bowden Formation assemblages. This percentage appears to increase significantly upsection within the lower Old Pera beds. Mann-Whitney U-tests indicate that significantly higher percentages of extant species occur in assemblages A to D than in assemblages E to H ($Z = -2.309$, $p = .0209$). The increase can be attributed to a greater abundance and diversity of branching *Stylophora* lower in the Old Pera beds section, and to a greater abundance of branching *A. cervicornis* higher in the section.

COMPARISONS WITH THE MANCHIONEAL AND HOPE GATE FORMATIONS ON THE JAMAICAN NORTH COAST

During June 1994, we also made collections of zooxanthellate scleractinians in the Manchioneal Formation near Port Antonio, and in the Hope Gate Formation near Rio Bueno and Discovery Bay (Fig. 1). In the Port Antonio area, we made collections at 12 sites on Folly Point (one in the Navy Island Member, 11 in the overlying rubbly Manchioneal Formation limestones) and three sites on Navy Island (one in the Navy Island Member, two in the Manchioneal Formation). In the Rio Bueno area, we made collections at four sites within 5 m of sea level on the eastern side of Rio Bueno Harbour, at six sites having elevations of 5-15 m within the cliff at the edge of the second or 30 m

terrace described by Land (1973), and at four sites having elevations of 30-50 m along the terrace surface south of the cliff. Study of microfossils in the Manchioneal Formation of the Port Antonio area has suggested that the Navy Island Member is Plio-Pleistocene in age or 1.9-1.6 Ma (Robinson & Lamb, 1970; Aubry, 1993). In addition, Robinson & Lamb (1970) used palaeomagnetic data to propose a correlation of the Navy Island Member to the Olduvai subchron (C2N, 1.95-1.77 Ma). This age is confirmed with a correlation to the *Calcidiscus macintyrei* Subzone of Gartner (1977) by Aubry (1993). The overlying Manchioneal Formation is earliest Pleistocene (~2.0-1.4 Ma) based on the data of Kohl (1992) adjusted to the Berggren *et al.* (1995b) timescale. Study of strontium isotopes has suggested that the Hope Gate Formation is latest Pliocene to earliest Pleistocene (Land, 1991). Our collections in the Port Antonio and Rio Bueno areas were made in a similar manner as those in the Bowden-Old Pera sequence, and sites were defined using the same criteria. A total of 258 specimens (34 species) were identified in the Port Antonio area collections, and 197 specimens (29 species) in the Rio Bueno area collections (Table 2).

In contrast to the Bowden-Old Pera sequence (Fig. 3), all of species in the Port Antonio area collections and 21 out of the 28 species (75%) in the Hope Gate Formation collections are extant (Table 2). Species with massive colony shapes dominate both the Port Antonio faunas (52.9% in the Navy Island Member; 63.6% in the Manchioneal Formation) and the Hope Gate fauna (50%), with free-living species being relatively unimportant. Unlike the Bowden-Old Pera sequence, species of the genera *Diploria* and *Montastraea* prevail, and platy species (in particular of *Agaricia* and *Mycetophyllia*) make up a significantly higher proportion of the fauna. Although slightly higher in the Navy Island Member, percentages of branching species are similar in the Bowden, Old Pera and north coast collections.

The similarities in geologic ages and differences in colony shapes suggest that the variation in taxonomic composition among the five faunas listed in Table 2 may be environmental. The relatively high number of massive coral species in the Port Antonio collections implies exposed shallow to intermediate depth (< 20 m) forereef conditions. However, studies of echinoderms and brachiopods in the Manchioneal Formation (Harper *et al.*, 1995; Donovan & Embden, 1996) indicate water depths of > 100 m, suggesting that the corals may have been transported from shallower reef depths. The Hope Gate assemblages have similarly high proportions of massive species, and also contain slightly higher proportions of platy and free-living species, again indicating deeper (15-25 m) forereef conditions.

The seven extinct species in the Hope Gate Formation include three branching species (*Stylophora granulata, S. minor, Caulastraea portoricensis*), one massive species (*Montastraea cylindrica*), and three free-living species (*Manicina* sp. C, *Trachyphyllia bilobata, Placocyathus*

variabilis). All of these species, except *M. cylindrica*, occur in the Bowden-Old Pera sequence, indicating that the extinct Hope Gate species represent a subset of the extinct Bowden-Old Pera fauna. The transitional nature of the Old Pera and Hope Gate faunas between the predominantly extinct Bowden fauna and extant Manchioneal fauna is further supported by detrended correspondence analysis (Fig. 6).
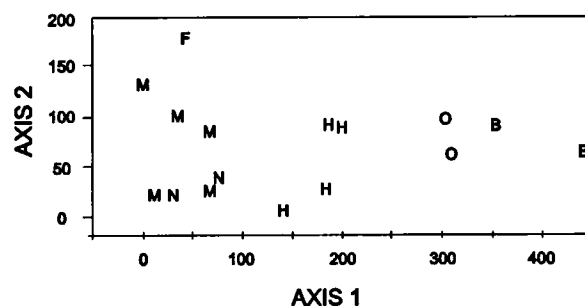

Fig. 6. Scatterplot of the first two axes determined by detrended correspondence analysis (DCA) of coral mega-assemblages in the Bowden shell bed (B) [3.8-2.7 Ma], Old Pera beds (O) [3-1.8 Ma], Hope Gate Formation (H) [1.8-1 Ma], Navy Island Member of the Manchioneal Formation (N) [1.9-1.6 Ma], Manchioneal Formation limestones (M) [2-1.4 Ma], and Falmouth Formation (F) [~125 Ka]. Each mega-assemblage consisted of all specimens collected within a stratigraphic unit that was 3-5 m high and 300-500 m wide. The analysis was run using relative abundance codes as defined in Budd *et al.* (1998) using PC-ORD, version 2.0 (McCune & Mefford, 1995). Visual examination of the plot suggests that axis 1 is related to % extinct species. Despite the overlap in ages of the Old Pera beds, Hope Gate Formation, and Manchioneal Formation, the three faunas appear at different stages of faunal transition.

In general, the high percentage of extinct corals in the Bowden-Old Pera sequence is due to the high numbers of free-living corals, which were more susceptible to extinction during Plio-Pleistocene time (Johnson *et al.*, 1995; Budd *et al.*, 1996).

THE BOWDEN FAUNA AND ITS EVOLUTIONARY SIGNIFICANCE

Study of museum collections from the Bowden shell bed increases the total number of species known from 24 to 38 species (Table 3). This number is approximately one-third of the 111 species estimated to have lived in the Caribbean as a whole between 4-1.5 Ma. With this addition, the proportions of extant species and of species with different colony shapes in the Bowden Formation remain approximately the same: nine of the 38 species (23.7%) are extant, 18 (47.4%) are free-living, 11 (28.9%) are massive, and

nine (23.7%) are branching.

A survey of the 82 Neogene to Recent Caribbean stratigraphic units in the 1996 Cenozoic Coral Database (CCD) compiled by Budd & Johnson (1997), reveals unusually high numbers of global last occurrences in the Bowden-Old Pera sequence (Table 4). Eight of the 38 coral species (21.0%) in the sequence have global last occurrences in the Bowden Formation, and 18 of the 37 species (48.6%) have global last occurrences in the Old Pera Beds or in units of equivalent age elsewhere in the Caribbean (most importantly, the Lomas del Mar reef trend near Limon, Costa Rica, and the Bahamas Drilling Project cores). These last occurrences involve range extensions of one or more million years in eleven free-living species; six species of *Manicina*, four species of *Placocyathus* and one species of *Antillia*.

Eight of the 38 species (21.0%) also have global first occurrences in the Bowden Formation or in units of equivalent age elsewhere in the Caribbean (most importantly, the Quebrada Chocolate and Buenos Aires reef trends near Limon, Costa Rica). Only one first occurrence involves a range extension of more than a million years; *Scolymia lacera*. With the exception of *Acropora* sp. Z, most species in the sequence appear to have had wide geographic distributions.

CONCLUSIONS

The large numbers of last occurrences in the Bowden-Old Pera sequence, and the contrast in taxonomic composition with the reef coral fauna of the north coast of Jamaica, suggest that the Bowden-Old Pera sequence may have served as one of the last refuges for Neogene Caribbean reef corals, especially free-living forms, before their extinction during Plio-Pleistocene time. The differences with the north coast fauna, in particular, suggest that reef communities in exposed settings established a modern aspect faster than their counterparts in protected environments. Faunal change associated with Plio-Pleistocene Caribbean turnover occurred at different times and rates, and followed different pathways at different Jamaican locations.

ACKNOWLEDGEMENTS

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Coral Assem blage	Stratigraphic Unit	AB94 localities	Equivalent ER localities	Number of Species	Number of Specimens
A	Bowden Fm.	12-14	10-15m ne of ER140	14	28
B	Bowden Fm.	10,11	140	9	39
C	Bowden Fm.	1,2	180	15	71
D	Old Pera beds	48,49	523, 1125	12	27
E	Old Pera beds	50,51	530, 1126	10	19
F	Old Pera beds	7-9,52	524, 1127, 1128	16	40
G	Old Pera beds	4-6,53,54	531,1130, 1131	19	53
H	Old Pera beds	45,55	532	11	17

Table 1.   List of our 1994 coral collecting sites in the Bowden Fm. – Old Pera beds sequence. AB, Ann Budd; ER, Edward Robinson (see Robinson, 1969).

Family	Genus	Species	CCD species ID no.	Colony shape	Survivor ship	Bowden shell bed	Old Pera beds	Navy Is Mem, Port Antonio	Manchioneal Fm, Port Antonio	Hope Gate Fm, Discovery Bay
Astrocoeniidae	*Stephanocoenia*	*intersepta*	002	massive	extant		x		x	x
Astrocoeniidae	*Stephanocoenia*	*duncani*	003	massive	extinct		x			
Pocilloporidae	*Stylophora*	*affinis*	005	branching	extinct		x			
Pocilloporidae	*Stylophora*	*granulata*	007	branching	extinct		x			x
Pocilloporidae	*Stylophora*	*minor*	009	branching	extinct		x			x
Pocilloporidae	*Stylophora*	*monticulosa*	010	branching	extinct	x	x			
Pocilloporidae	*Pocillopora*	*crassoramosa*	015	branching	extinct		x			
Pocilloporidae	*Madracis*	*mirabilis*	020	branching	extant		x	x	x	
Acroporidae	*Acropora*	*cervicornis*	022	branching	extant	x	x	x	x	x
Acroporidae	*Acropora*	*palmata*	023	branching	extant	x		x	x	x
Acroporidae	*Acropora*	sp.Z	026.5	branching	extinct	x				
Agariciidae	*Agaricia*	*lamarcki*	030	platy	extant			x	x	x
Agariciidae	*Agaricia*	*undata*	032	platy	extant				x	x
Agariciidae	*Undaria*	*agaricites*	033	platy	extant		x	x	x	x
Agariciidae	*Undaria*	*crassa*	034	massive	extant		x		x	
Agariciidae	*Helioseris*	*cucullata*	043	platy	extant				x	
Siderastreidae	*Siderastrea*	*radians*	056	massive	extant				x	
Siderastreidae	*Siderastrea*	*siderea*	058	massive	extant		x	x	x	x
Poritidae	*Porites*	*astreoides*	063	massive	extant	x	x	x	x	x
Poritidae	*Porites*	*portoricensis*	065	branching	extinct		x			
Poritidae	*Porites*	*baracoaensis*	069	branching	extinct	x	x			
Poritidae	*Porites*	*branneri*	070	massive	extant		x			
Poritidae	*Porites*	*divaricata*	075	branching	extant		x			
Poritidae	*Porites*	*furcata*	076	branching	extant		x	x		x
Poritidae	*Porites*	*porites*	077	branching	extant			x	x	
Poritidae	*Goniopora*	*imperatoris*	080	massive	extinct		x			
Faviidae	*Caulastraea*	*portoricensis*	083	branching	extinct		x		x	x
Faviidae	*Diploria*	*clivosa*	094	massive	extant				x	
Faviidae	*Diploria*	*labyrinthiformis*	095	massive	extant				x	x
Faviidae	*Diploria*	*strigosa*	097	massive	extant				x	x
Faviidae	*Manicina*	*aff.areolata*	100.5	free-living	extinct	x	x			
Faviidae	*Manicina*	*mayori*	101	massive	extant			x	x	x
Faviidae	*Manicina*	*puntagordensis*	102	free-living	extinct	x	x			
Faviidae	*Manicina*	*grandis*	103	free-living	extinct	x				
Faviidae	*Thysanus*	*navicula*	104	free-living	extinct		x			

Table 2.   List of zooxanthellate scleractinian coral species identified in our 1994 collections.

Family	Genus	Species	No.	Form	Status					
Faviidae	Manicina	sp.A	105	free-living	extinct	x				
Faviidae	Manicina	sp.B	106	free-living	extinct	x				
Faviidae	Manicina	sp.C	107	free-living	extinct	x	x			x
Faviidae	Thysanus	excentricus	110	free-living	extinct	x	x			
Faviidae	Thysanus	corbicula	111	free-living	extinct		x			
Faviidae	Colpophyllia	natans	114	massive	extant		x	x	x	x
Faviidae	Montastraea	annularis	116	massive	extant			x	x	
Faviidae	Montastraea	faveolata	117	massive	extant					x
Faviidae	Montastraea	franksi	118	massive	extant				x	x
Faviidae	Montastraea	limbata-1	121.1	massive	extinct		x			
Faviidae	Montastraea	cavernosa-2	126	massive	extant			x	x	x
Faviidae	Montastraea	cylindrica	128	massive	extinct					x
Faviidae	Solenastrea	bournoni	131	massive	extant	x				
Trachyphyllidae	Trachyphyllia	bilobata	135	free-living	extinct	x				x
Meandrinidae	Meandrina	braziliensis	138	free-living	extant	x	x			
Meandrinidae	Meandrina	meandrites	139	massive	extant			x	x	x
Meandrinidae	Meandrina	sp.A	139.5	massive	extant		x			
Meandrinidae	Placocyathus	alveolus	140	free-living	extinct	x	x			
Meandrinidae	Placocyathus	barretti	141	free-living	extinct	x	x			
Meandrinidae	Placocyathus	costatus	142	free-living	extinct	x	x			
Meandrinidae	Placocyathus	variabilis	144	free-living	extinct	x	x			x
Meandrinidae	Dichocoenia	stokesi	148	massive	extant			x	x	x
Meandrinidae	Dichocoenia	stellaris	149	massive	extant			x	x	
Meandrinidae	Dichocoenia	tuberosa	150	massive	extinct		x			
Meandrinidae	Dendrogyra	cylindricus	151	massive	extant				x	
Mussidae	Antillia	dentata	153	free-living	extinct		x			
Mussidae	Antillia	gregorii	154	free-living	extinct	x				
Mussidae	Scolymia	cubensis	155	massive	extant	x			x	
Mussidae	Scolymia	lacera	157	massive	extant				x	x
Mussidae	Mussa	angulosa	158	branching	extant				x	
Mussidae	Isophyllastrea	rigida	165	massive	extant				x	
Mussidae	Mycetophyllia	danaana	168	massive	extant				x	
Mussidae	Mycetophyllia	lamarckiana	170	platy	extant				x	x
Mussidae	Mycetophyllia	reesi	171	platy	extant					x
Caryophylliidae	Eusmilia	fastigiata	173	branching	extant		x	x	x	
				total # localities		7	15	2	13	14
				total # specimens		138	156	30	228	197
				total # species		24	37	17	33	28
				# extant species		6	14	17	32	21
				# free-living species		16	12	0	0	3
				# branching species		5	13	6	7	6
				# massive species		3	11	9	21	14
				# platy species		0	1	2	5	5

Table 2.   List of zooxanthellate scleractinian coral species identified in our 1994 collections (continued).

CCD species ID no.	Genus	Species	Present Study	Duncan 1863,1864 (BMNH)	Vaughan 1901,1919 (USNM)	Wells coll. (SUI)	Vokes coll. (USNM) loc. T705	UWI coll.	UF coll. (loc. XJ002)
003	Stephanocoenia	duncani		x?	x		x		
007	Stylophora	granulata		H	x			x	x
009	Stylophora	minor							x
010	Stylophora	monticulosa	x						x
020	Madracis	mirabilis (*)		x	x				
022	Acropora	cervicornis (*)	x						
023	Acropora	palmata (*)	x						
026.5	Acropora	sp.Z	x		x			x	x
058	Siderastrea	siderea (*)		x (H)	x				
063	Porites	astreoides (*)	x						
069	Porites	baracoaensis	x	x?	x				x
080	Goniopora	imperatoris		x?	x			x	
083	Caulastraea	portoricensis						x	
099	Diploria	sp.A							x
100.5	Manicina	aff.areolata	x						
102	Manicina	puntagordensis	x						
103	Manicina	grandis	x				x		x
104	Thysanus	navicula	x						x
105	Manicina	sp.A	x					x	
106	Manicina	sp.B	x					x	
107	Manicina	sp.C	x					x	
109	Thysanus	sp.A						x	
110	Thysanus	excentricus	x	H (H)	x	x	x	x	x
111	Thysanus	corbicula	x		x	x	x	x	
121.1	Montastraea	limbata-1				x	x		
124	Montastraea	canalis					x		
131	Solenastrea	bournoni (*)	x	x (H)			x		
135	Trachyphyllia	bilobata	x	x (H)		x		x	
138	Meandrina	braziliensis (*)	x					x	
140	Placocyathus	alveolus	x	H	x	x	x	x	x
141	Placocyathus	barretti	x	H (H)	x		x	x	x
142	Placocyathus	costatus	x				x	x	x
143	Placocyathus	? trinitatis						x	
144	Placocyathus	variabilis	x			x	x	x	x
150	Dichocoenia	tuberosa						x	
154	Antillia	gregorii	x	x	H*			x	x
155	Scolymia	cubensis (*)	x		x	x		x	
157	Scolymia	lacera (*)						x	
		Total	24	13	13	7	11	21	14

Table 3.   Complete list of zooxanthellate scleractinian species known from the Bowden shell bed. H=holotype, (H)= holotype of a synonymized species, H*=holotype of another museum, (*)=extant species.

CCD species ID no.	Genus	Species	Bowden, Old Pera Occurrences	Global First Occurrence excluding Bowden-Old Pera sequence	Global Last Occurrence excluding Bowden-Old Pera sequence	Global First Occurrence in Bowden Fm (3.8-2.7 Ma) or Old Pera beds (3-1.8 Ma)	Global Last Occurrence in Bowden Fm (3.8-2.7 Ma) or Old Pera beds (3-1.8 Ma)
002	Stephanocoenia	intersepta	OP	Pinecrest Ss, Florida (3.5-3 Ma)	Recent		
003	Stephanocoenia	duncani	B,OP	Anguilla Fm, Anguilla (22-16.2 Ma)	Lomas del Mar, Cos.Rica (1.9-1.5 Ma)		=OP
005	Stylophora	affinis	OP	Gurabo Fm, Dom. Rep. (8.3-7.5 Ma)	La Cruz Fm, Cuba (3.5-1.6 Ma)		=OP
007	Stylophora	granulata	B,OP	Emperador Lm, Panama (22-17.6 Ma)	Unda-2, Bahamas (1.8-1.7 Ma)		
009	Stylophora	minor	B,OP	Tampa Fm, FL (23.7-22 Ma)	Unda-3, Bahamas (1.9-1.8 Ma)		=OP
010	Stylophora	monticulosa	B,OP	Baitoa Fm, Dom.Rep. (17.3-13.1 Ma)	Unda-2, Bahamas (1.8-1.7 Ma)		
015	Pocillopora	crassoramosa	OP	Baitoa Fm, Dom.Rep. (17.3-13.1 Ma)	Mao Fm, Dom.Rep. (3.7-3.4 Ma)		OP
020	Madracis	mirabilis	B,OP	Tamana Fm, Trinidad (15-11.2 Ma)	Recent		
022	Acropora	cervicornis	B,OP	Q. Chocolate, Cos.Rica (3.5-3.2 Ma)	Recent	=B	
023	Acropora	palmata	B	Buenos Aires, Cos.Rica (3.2-2.9 Ma)	Recent	=B	
026.5	Acropora	sp.Z (*)	B	none	none	B	B
033	Undaria	agaricites	OP	Cercado Fm, Dom. Rep. (8.3-7.5 Ma)	Recent		
034	Undaria	crassa	OP	Cercado Fm, Dom.Rep. (7.5-5.6 Ma)	Recent		
058	Siderastrea	siderea	B,OP	Baitoa Fm, Dom.Rep. (17.3-13.1 Ma)	Recent		
063	Porites	astreoides	B,OP	Buenos Aires, Cos.Rica (3.2-2.9 Ma)	Recent	=B	
065	Porites	portoricensis	OP	Tampa Fm, FL (23.7-22 Ma)	Lomas del Mar, Cos.Rica (1.9-1.5 Ma)		=OP
069	Porites	baracoaensis	B,OP	Emperador Lm, Panama (22-17.6 Ma)	Lomas del Mar, Cos.Rica (1.9-1.5 Ma)		=OP
070	Porites	branneri	OP	Pinecrest Ss, FL (3.5-3 Ma)	Recent		
075	Porites	divaricata	OP	Caloosahatchee Fm, FL (1.8-1.6 Ma)	Recent	OP	
076	Porites	furcata	OP	Pinecrest Ss, FL (3.5-3 Ma)	Recent		
080	Goniopora	imperatoris	B,OP	Tampa Fm, FL (23.7-22 Ma)	Unda-3, Bahamas (1.9-1.8 Ma)		=OP
083	Caulastraea	portoricensis	B,OP	Lirio Lm, Mona (11.2-5.3 Ma)	Lomas del Mar, Cos.Rica (1.9-1.5 Ma)		=OP
099	Diploria	sp.A	B	Gurabo Fm, Dom.Rep. (7.5-5.6 Ma)	Mao Fm, Dom.Rep. (4-3.7 Ma)		=B
100.5	Manicina	aff.areolata	B,OP	Gurabo Fm, Dom.Rep. (5.6-4.5 Ma)	Mao Fm, Dom.Rep. (4-3.7 Ma)		=B
102	Manicina	puntagordensis	B,OP	Buenos Aires, Cos.Rica (3.2-2.9 Ma)	Lomas del Mar, Cos.Rica (1.9-1.5 Ma)	=B	=OP
103	Manicina	grandis	B	Cercado Fm, Dom.Rep. (8.3-7.5 Ma)	Mao Fm, Dom.Rep. (4-3.7 Ma)		=B
104	Thysanus	navicula	B,OP	Cercado Fm, Dom.Rep. (7.5-5.6 Ma)	Mao Fm, Dom.Rep. (4-3.7 Ma)		OP
105	Manicina	sp.A	B	Lirio Lm, Mona (11.2-5.3 Ma)	Gurabo Fm, Dom.Rep. (4.5-4 Ma)		B
106	Manicina	sp.B	B	Gurabo Fm, Dom.Rep. (8.3-7.5 Ma)	Gurabo Fm, Dom.Rep. (4.5-4 Ma)		B
107	Manicina	sp.C	B,OP	Cercado Fm, Dom.Rep. (7.5-5.6 Ma)	Mao Fm, Dom.Rep. (4-3.7 Ma)		OP
109	Thysanus	sp.A	B	Q. Chocolate, Cos.Rica (3.5-3.2 Ma)	Lomas del Mar, Cos.Rica (1.9-1.5 Ma)	=B	
110	Thysanus	excentricus	B,OP	Gurabo Fm, Dom.Rep. (7.5-5.6 Ma)	Clino-4, Bahamas (1.9-1.8 Ma)		=OP
111	Thysanus	corbicula	B,OP	Chipola Fm, FL (18-15 Ma)	Caloosahatchee Fm, FL (1.8-1.6 Ma)		=OP
114	Colpophyllia	natans	OP	Gurabo Fm, Dom.Rep. (5.6-4.5 Ma)	Recent		
121.1	Montastraea	limbata-1	B,OP	?Tamana Fm, Trinidad (14.8-11.5 Ma)	Lomas del Mar, Cos.Rica (1.9-1.5 Ma)		
124	Montastraea	canalis	B	Tampa Fm, FL (23.7-22 Ma)	Lomas del Mar, Cos.Rica (1.9-1.5 Ma)		
131	Solenastrea	bournoni	B	Tampa Fm, FL (23.7-22 Ma)	Recent		
135	Trachyphyllia	bilobata	B	Tampa Fm, FL (23.7-22 Ma)	Clino-4, Bahamas (1.8-1.6 Ma)		
138	Meandrina	brazilensis	B,OP	Cercado Fm, Dom.Rep. (8.3-7.5 Ma)	Recent		
139.5	Meandrina	sp.A	OP	Gurabo Fm, Dom.Rep. (5.6-4.5 Ma)	Recent		
140	Placocyathus	alveolus	B,OP	Gurabo Fm, Dom.Rep. (7.5-5.6 Ma)	Pinecrest Ss, FL (3.5-3 Ma)		OP
141	Placocyathus	barretti	B,OP	Pinecrest Ss, FL (3.5-3 Ma)	Pinecrest Ss, FL (3.5-3 Ma)	=B	OP
142	Placocyathus	costatus	B,OP	Gurabo Fm, Dom.Rep. (8.3-7.5 Ma)	Mao Fm, Dom.Rep. (3.7-3.4 Ma)		OP
143	Placocyathus	? trinitatis	B	Manzanilla Fm, Trinidad (11.2-5.3 Ma)	Gurabo Fm, Dom.Rep. (4.5-4 Ma)		B
144	Placocyathus	variabilis	B,OP	Baitoa Fm, Dom.Rep. (17.3-13.1 Ma)	Lomas del Mar, Cos.Rica (1.9-1.5 Ma)		=OP
150	Dichocoenia	tuberosa	B,OP	Gurabo Fm, Dom.Rep. (7.5-5.6 Ma)	Lomas del Mar, Cos.Rica (1.9-1.5 Ma)		=OP
154	Antilla	gregorii	B	Tampa Fm, FL (23.7-22 Ma)	Tampa Fm, FL (23.7-22 Ma)		B
155	Scolymia	cubensis	B	Gurabo Fm, Dom.Rep. (7.5-5.6 Ma)	Recent		
157	Scolymia	lacera	B	Lomas del Mar, Cos.Rica (1.9-1.5 Ma)	Recent	B	
173	Eusmilia	fastigiata	OP	Pinecrest Ss, FL (3.5-3 Ma)	Recent		

Table 4. First and last Occurrence in the Bowden – Old Pera sequence. B, Bowden; OP, Old Pera; (*) known only from the Bowden – Old Pera sequence.

PLATE 1

Common and abundant zooxanthellate scleractinian species in the Bowden shell bed (in taxonomic order). All specimens were collected from the Bowden shell bed, except Fig. b, which was collected from the Old Pera beds approximately 1 km south of the shell bed.

Figs a, b.   *Stylophora granulata* Duncan, 1864; a — USNM 324779, branch fragment, x 0.9; b — SUI 92037 (CCD 4374), CCD locality AB94-53 (Old Pera beds), branch fragment, x 0.9.

Fig. c.   *Stylophora monticulosa* Vaughan *in* Vaughan & Hoffmeister, 1925; UWIGM 11512, UWI locality 10, branch fragment, x 1.

Fig. d.   *Acropora* sp. Z; SUI 92038 (CCD 4391), locality AB94-11, branch fragment, x 0.9.

Fig. e.   *Porites astreoides* Lamarck, 1816; SUI 92041 (CCD 4371), CCD locality AB94-13, whole colony, x 0.65.

Fig. f.   *Goniopora imperatoris* Vaughan, 1919; USNM 65473, colony side, x 1.2.

Figs g, h.   *Manicina grandis* (Duncan, 1864); g — USNM 65474, USGS locality 2580, calical surface, x 0.9; h — USNM 65464, same specimen as Fig. g, side view, x 0.9.

Figs i, j.   *Manicina* sp. C; UWIGM 11519, UWI locality 10; i — calical surface, x 0.9; j — side view, x 0.9.

Figs k, l.   *Thysanus excentricus* Duncan, 1863; SUI 90997, CCD locality AB94-11; k — calical surface, x 0.9; l — side view, x 0.9.

Figs m, n.   *Thysanus elegans* Duncan *in* Duncan & Wall, 1865 (? = *T. excentricus*); USNM 63325, USGS locality 2580; m — calical surface, x 0.9; n — side view, x 0.9.
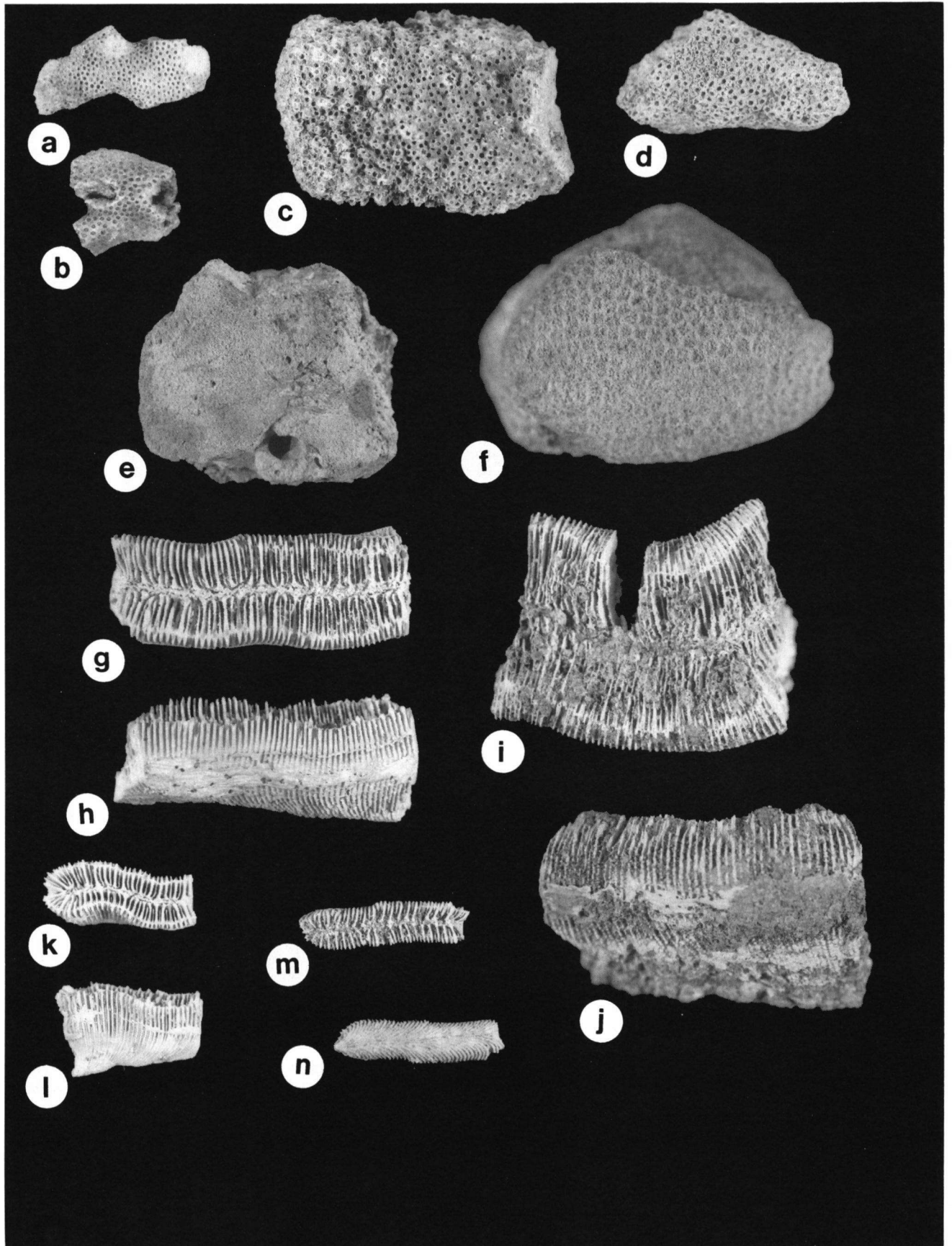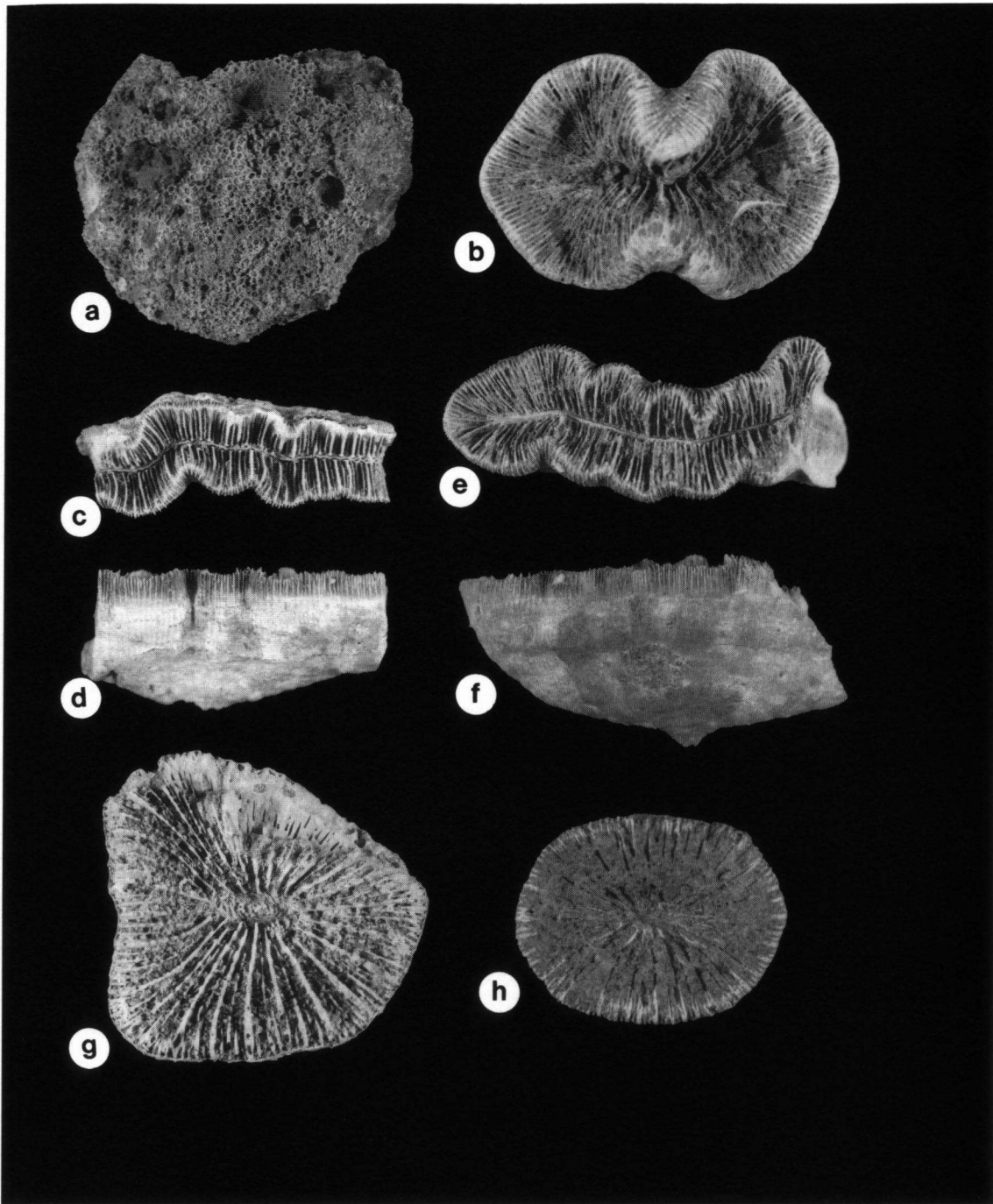
PLATE 1

PLATE 2

PLATE 2

Common and abundant zooxanthellate scleractinian species in the Bowden shell bed (in taxonomic order). All specimens were collected from the Bowden shell bed, except Figs b and g which were collected from the Bowden Formation (locality ER 180) approximately 0.75 km south of the shell bed.

Fig. a.   *Solenastrea bournoni* Milne Edwards & Haime, 1849; SUI 93101 (CCD 4366), CCD locality AB94-13, whole colony, x 0.5.
Fig. b.   *Trachyphyllia bilobata* (Duncan, 1863); SUI 92040, Wells Colln, locality ER 180, calical surface, x 0.65.
Figs c, d. *Placocyathus alveolus* (Duncan, 1863); USNM 95334, Tulane locality 705; c — calical surface, x 0.9; d — side view, x 0.9.
Figs e, f. *Placocyathus barretti* Duncan, 1863; USNM 63371, USGS locality 2580; e — calical surface, x 0.65; f — side view, x 0.65.
Fig. g.   *Scolymia cubensis* (Milne Edwards & Haime, 1849); SUI 92039, Wells Colln, locality ER 180, calical surface, x 0.65.
Fig. h.   *Antillia gregorii* Vaughan, 1901; USNM 65469, USGS locality 2580, calical surface, x 1.