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# A Paleobiotic Survey of Caribbean Faunas from the Neogene of the Isthmus of Panama

edited by

Laurel S. Collins and Anthony G. Coates

**Panama Paleontology Project**

**Paleontological Research Institution**
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**Ithaca, New York, 14850 U.S.A.**

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# INTRODUCTION

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A fundamental question in biology concerns the extent to which populations and communities are affected by geographic isolation and environmental change, a full comprehension of which must include understanding environmental conditions and biodiversity of the past. The main research goal of the project that produced this volume is an assessment of patterns of changing marine invertebrate faunas of tropical America over the last ~10 million years, for the purpose of determining the impacts of environmental change and genetic isolation on large-scale evolution and ecologic systems. This multitaxonomic paleobiotic survey takes advantage of a "natural experiment," the Miocene constriction of the Caribbean-Pacific seaway and the Pliocene emergence of the Isthmus of Panama, which resulted in biotic isolation and changes in oceanic conditions on opposite sides. We initially concentrated on southern Central America because the bulk of evidence indicates that this is where final isolation of the tropical Atlantic and Pacific occurred. In this region, the biological effects are likely to have been most pronounced and directly relatable to the physical, sedimentary record of isthmian emergence. A remarkably complete record of these events is preserved in Neogene sediments of the region, including abundant, diverse and well-preserved macrofaunas and microfaunas. In addition, the Recent lies at the end of this time range, providing extant collections for comparative anatomical and molecular studies.

The Panama Paleontology Project (PPP), was initiated to make the systematic, regional fossil collections and fine-scaled chronologic framework necessary for these investigations. All geographic, stratigraphic, and taxonomic data are integrated in the PPP Database. From these and and other data, paleontologists are documenting biodiversity, biogeographic change, and the origination and extinction of tropical American organisms, and relating these to patterns of environmental and tectonic changes.

## THE PANAMA PALEONTOLOGY PROJECT

The PPP is a geographically, chronologically and logistically large-scaled endeavor that has taken considerable time and effort to develop. The advantage of a coordinated project is that it can take a multitaxonomic, integrated approach to investigating evolutionary and environmental processes. The project currently involves 35 scientists from 20 institutions in 7 countries (see the PPP internet site at http://www.fiu.edu/˜collinsl/), although many more have participated during its existence (Table 1). The PPP organizes expeditions to collect fossils and measure geologic sections; prepares and curates macrofossils and microfossils from standardized, random samples; assigns ages using microfossils, paleomagnetics and radiometric dating; and reconstructs paleoenvironments based on microfossil and macrofossil assemblages, sedimentology, and stable isotopes. The maintenance and development of the PPP Database and the extensive collections support longer term taxonomic, systematic, ecologic and evolutionary studies. Below we describe the organization of the project.

This formal collaboration began in 1986 with a reconnaissance survey of the Neogene geology of Panama by Jeremy Jackson and Anthony Coates. The objective was to determine whether the fossils were sufficiently abundant, both stratigraphically and geographically, for research on the evolutionary and ecological consequences of the rise of the Isthmus of Panama. In 1987, Peter Jung and Laurel Collins joined the project, which became known as the Panama Paleontology Project. This group, with the addition of Ann Budd in 1993, formed a steering committee to plan collecting expeditions, seek funds, devise guide-

Table 1.—Members*, field participants and assistants in the Panama Paleontology Project, 1986–1999.

| | | |
|---|---|---|
| | Steering Committee | |
| Ann Budd* | Hermatypic corals, taxonomy database | U.S.A. |
| Anthony Coates* | Stratigraphy | U.S.A. |
| Laurel Collins* | PPP Database, benthic foraminfera, stable isotopes | U.S.A. |
| Jeremy Jackson* | Scientific coordination, bryozoans, mollusks | U.S.A. |
| Peter Jung* | Mollusks | Switzerland |
| | Scientists | |
| Teresita Aguilar | Mollusks | Costa Rica |
| Orangel Aguilera* | Teleost fishes | Venezuela |
| Laurie Anderson* | Corbulid bivalves | U.S.A. |
| Marie-Pierre Aubry* | Calcareous nannofossils, biochronology | France |
| Guillermo Barbosa | Regional geology | Costa Rica |
| Peter Baumgartner | Tectonics | Switzerland |
| William Berggren* | Planktic foraminifera, biochronology | U.S.A. |
| Pamela Borne* | Ostracodes | U.S.A. |
| Laurel Bybell* | Calcareous nannofossils, biochronology | U.S.A. |
| Alan Cheetham* | Cheilostome bryozoans | U.S.A. |
| Stephen Cairns* | Ahermatypic corals | U.S.A. |
| Mathew Cotton* | Planktic foraminifera, biochronology | U.S.A. |
| Timothy Collins* | Gastropods, molecular biology | U.S.A. |
| Thomas Cronin* | Ostracodes | U.S.A. |
| John Dawson* | Ahermatypic corals | U.S.A. |
| Stephen Donovan* | Echinoids | England |
| Harry Dowsett* | Planktic foraminifera, paleoceanography | U.S.A. |
| Helena Fortunato* | Strombiniid gastropods, taxonomy database | Panama |
| Andrew Gale | Facies analysis | England |
| Dana Geary* | Strombid gastopods, stable isotopes | U.S.A. |
| Thor Hansen* | Mollusks | U.S.A. |
| Antoine Heitz | Mollusk curation and taxonomy | France |
| Nelson Jimenez | Calcareous nannofossils | Ecuador |
| Kenneth Johnson* | Hermatypic corals, data analysis | U.S.A. |
| Karl Kaufmann* | PPP Database | U.S.A. |
| Patricia Kelley* | Mollusks | U.S.A. |
| Susan Kidwell | Stratigraphy | U.S.A. |
| Michael Kunk | Radiometric dating (Ar39/40) | U.S.A. |
| Lorena Lanza | Regional geology | Nicaragua |
| Peter Marko* | Arcid bivalves, molecular biology | U.S.A. |
| Donald McNeill* | Magnetostratigraphy | U.S.A. |
| Jorge Mideros | Petroleum geologist | Ecuador |
| Daniel Miller* | Muricid gastropods, mollusk taxonomy | U.S.A. |
| Simon Mitchell | Stratigraphy and sedimentology | Jamaica |
| Richard Mooi* | Clypeasteroid echinoderms | U.S.A. |
| Galo Montenegro | Petroleum geologist | Ecuador |
| Ross Nehm* | Marginellid gastropods | U.S.A. |
| Florin Neumann | Dinoflagellates | Romania |
| Hiroshi Noda | Mollusks | Japan |
| Jorge Obando* | Regional sedimentation | Costa Rica |
| Luis Obando | Regional stratigraphy and geology | Costa Rica |
| Marta Ordoñez | Foraminifera, biostratigraphy | Ecuador |
| Dawn Peterson* | Ostracodes | U.S.A. |
| Stephen Schellenberg | Sr isotopes of reef corals | U.S.A. |
| Jay Schneider* | Cardiid bivalves | U.S.A. |
| John Sutter | Radiometric dating (Ar39/40) | U.S.A. |
| Paul Taylor* | Cyclostome bryozoans | England |
| Jane Terranes* | Stable isotopes of mollusks | U.S.A. |
| Jon Todd* | Polystirid gastropods | England |
| Pascal Tschudin* | Glycymerid bivalves | Switzerland |
| Italo Zambrano | Palynology | Ecuador |
| Jijun Zhang* | Planktic foraminifera, biochronology | Canada |
| | Research Assistants | |
| Dione R. de Aguilera | Sample processing for fishes | Venezuela |
| Raul Brito | Student assistant | Ecuador |
| Eric Brown | Field assistant | Panama |
| Martin Brunner | Student assistant | Switzerland |
| Magnolia Calderon | Sample processing | Panama |
| Rogelio Cansari | Field guide | Panama |
| Daniel Castañeda | Field guide | Panama |
| Sebastian Castillo | Boatman | Panama |
| Janet Coates | Field logistics | U.S.A. |
| John-Mark Coates | Field assistant | U.S.A. |
| Chena Cooke | Field logistics | Panama |
| Luis Cruz | Field assistant | Panama |
| James Diaz | Student assistant | U.S.A. |
| Beatrice Ferrenbach | Field logistics | Panama |
| Lucien Ferrenbach | Field logistics | Panama |
| Xenia Guerra | Research assistant | Panama |
| Karl Hansen | Photographer | U.S.A. |
| Huichan Lin | Nannofossil processing | U.S.A. |
| Dorotheo Machado | Field assistant | Panama |
| Claudia Mora | Field assistant | Costa Rica |
| Angelica Muñoz | Field guide | Nicaragua |
| Agustín Paladines | Student assistant | Ecuador |
| Rene Panchaud | Field assistant, collections manager | Switzerland |
| Betzabeth Rios | Sample processing | Panama |
| Fabricio Sierra | Student assistant | Ecuador |
| Omar Sugasti | Field assistant | Panama |
| Bridget Tompkins | Student assistant | U.S.A. |
| Sophia Velotti | Sample processing | Panama |
| Yira Ventocilla | Sample processing | Panama |
| Jamie Wineberg | Student assistant | U.S.A. |
| David West | Research vessel, Captain | Panama |

lines for preparing collections, coordinate studies of taxonomic groups, and organize joint publications. U. S. Geological Survey paleontologists Bybell (calcareous nannoplankton), Dowsett (planktic foraminifera) and Cronin (ostracodes), together with graduate student Cotton (planktic foraminifera), contributed the PPP's biostratigraphic foundation. The question of an adequate fossil record was answered affirmatively by Coates *et al.* in 1992.

Fossil collections are most useful to researchers when they reside at centralized locations. An agreement was signed between the Smithsonian Tropical Research Institute (STRI, the home institution of Jackson and Coates) and the Naturhistorisches Museum Basel (Jung's institution) that all of the mollusks and less abundant groups (crustaceans, echinoderms, brachiopods) would be prepared and accessioned in Basel, and that all bryozoans, corals, foraminifera, calcareous nannofossils, and ostracodes would be permanently housed, after study by the appropriate specialists, at the U.S. National Museum of Natural History, Washington D.C.

By 1990, growth in the volume and completeness of the collections required new procedures and a broadened taxonomic expertise. To census the macrofauna, full-time "factories" at STRI and Basel were established for processing bulk sediment samples taken at shell-rich sites. The data on locality, stratigraphy, age, sample processing, and identified taxa began to be tracked in the PPP Database designed by Kaufmann (Chapter 12) and Collins. New colleagues began to study PPP bryozoans (Cheetham), mollusks (Geary, Anderson, Schneider), corals (Cairns), and regional sedimentation (Obando).

Since 1993, the PPP has developed into two (overlapping) research groups, a division reflected in the two parts of this volume. The first group establishes a chronologic and paleoenvironmental framework for each region, and the second builds its paleobiological studies upon this framework. The stratigraphic part of the first group consists of Coates, Aubry (calcareous nannofossil biostratigraphy), Berggren and Zhang (planktic foraminiferal biostratigraphy), and McNeill (paleomagnetics). Within the constraints of the physical stratigraphy, the biostratigraphers use the evolutionary and paleoceanographic history of microfossils to establish a high-resolution chronology for stratigraphic sections. The ages of many sections are further refined by applying the chronology of paleomagnetic reversals. Paleoenvironmental determinations (Chapter 4) are based on the modern ecology of primarily benthic foraminifera (Collins), but also ostracodes (Borne, Cronin, Peterson), otoliths (Aguilera), ahermatypic corals (Cairns), and sedimentology.

The second PPP research group includes members conducting macrofossil and microfossil studies of evolution, biogeography and ecology. For the mollusks, by far the most diverse group, Jackson coordinates the analysis of faunal lists of genera and subgenera that have been taxonomically standardized by Heitz, Jung and Todd. Several molluscan clades with modern transisthmian distributions are being studied with morphometric and/or molecular techniques by Anderson, Fortunato, Jackson, Marko, Miller, Nehm, Schneider, Tshudin and Todd. Additional paleobiological research includes that of Aguilera (otoliths), Borne and Peterson (ostracodes), Donovan and Mooi (echinoderms), Budd, Johnson, and Stemann (reef corals), Cairns and Dawson (ahermatypic corals), Cheetham, Jackson and Taylor (bryozoans), and Collins (benthic foraminifera). In addition to the PPP Database of information about locality, stratigraphy, age, and taxon occurrence (Kaufmann and Collins), Budd designed and implemented a taxonomic database (Nmita) that contains information such as photographic and scanning electron micrograph images on PPP and other tropical American paleontological collections.

To obtain comparative Caribbean and Eastern Pacific collections, expeditions were undertaken more or less equally to both sides of the southern Central American isthmus during the first five years of the PPP (Table 2). In the next six years, most expeditions focused on the relatively complete and fossiliferous Caribbean sections of the Limon region of Costa Rica, and the Bocas del Toro and Colon regions of Panama. Many new formations were described, dated, and collected in detail to yield unparalleled collections of fossils from different stratigraphic levels and facies. The Caribbean stratigraphy and collections form the focus of this volume.

In contrast to the Caribbean coast, the Pacific coast from the Darien (eastern Panama) to Nicaragua has yielded sequences that are less continuous chronologically and not comparable in age, environment, and taxonomic diversity with the Caribbean faunas. The most important Pacific sequences are in the Darien (Middle-Upper Miocene) and the Burica Peninsula (Pliocene-Lower Pleistocene). Recently, to compensate for this inadequate record, the PPP began fieldwork in Ecuador, where richly fossiliferous, Neogene sequences extend from the coast to the Andean foothills of the Borbon and Manabi basins. We hope to summarize all these sequences in a companion volume on the Neogene of the Pacific coast.

## BIODIVERSITY AND SCALE

The large scale of the Panama Paleontology Project is the main characteristic that differentiates it from other field-based paleontological projects. To study the diversity and distribution of taxa within a tropical ocean basin over ~10 million years at a relatively fine chronological scale requires years of constructing a regional stratigraphy and collecting and identifying fossils. For most taxonomic groups, collections have only recently become sufficient to calculate biodiversity re-

Table 2.—PPP expeditions, 1986–1999.

| | Begun | Country | Region | Mode |
|---|---|---|---|---|
| 1 | 1/13/86 | Panama | Colon | truck |
| | 1/16/86 | Panama | Burica Peninsula | truck |
| | 1/18/86 | Panama | Bocas del Toro | truck, canoe |
| 2 | 3/21/86 | Panama | Burica Peninsula | truck |
| 3 | 2/9/87 | Panama | Lake Bayano | truck, boat |
| | 2/19/87 | Panama | Burica Peninsula | truck |
| 4 | 8/4/87 | Panama | North coast | STRI *R/V* |
| | 8/7/87 | Panama | Bocas del Toro | |
| | 8/18/87 | Panama | Colon | truck |
| 5 | 3/13/88 | Costa Rica | Burica Peninsula, Nicoya Peninsula | STRI *R/V* |
| | 3/27/88 | Costa Rica | Limon | truck |
| 6 | 5/30/88 | Panama | Bocas del Toro | STRI *R/V* |
| | 6/12/88 | Panama | Colon | truck |
| 7 | 1/12/89 | Costa Rica | Burica Peninsula | foot, horses |
| 8 | 4/2/89 | Costa Rica | Limon | truck |
| 9 | 3/16/90 | Costa Rica | Osa Peninsula, Nicoya Peninsula | foot, truck, horses |
| 10 | 7/12/90 | Panama | Darien | truck, canoe |
| 11 | 1/15/91 | Panama | Darien | truck, canoe |
| 12 | 1/4/92 | Panama | Colon | truck |
| | 1/8/92 | Costa Rica | Limon | truck |
| | 1/12/92 | Costa Rica | Burica Peninsula | truck |
| 13 | 11/28/92 | Panama | Colon | truck |
| | 12/1/92 | Costa Rica | San Carlos | truck |
| | 12/3/92 | Nicaragua | Managua | truck |
| 14 | 5/4/93 | Panama | Darien | canoe |
| 15 | 6/13/93 | Panama | Colon | truck |
| 16 | 7/13/93 | Costa Rica | Limon | car |
| 17 | 8/1/93 | Panama | Bocas del Toro | motor boat |
| 18 | 3/6/94 | Panama | Darien | canoe |
| 19 | 3/20/94 | Panama | Colon | truck |
| 20 | 3/29/94 | Costa Rica | Golfo Dulce | truck |
| | 3/31/94 | Panama | Burica Peninsula | truck |
| 21 | 4/7/94 | Panama | Bocas del Toro | motor boat |
| | 4/8/94 | Panama | Burica Peninsula | truck |
| 22 | 11/3/94 | Panama | Bocas del Toro | motor boat |
| 23 | 2/22/95 | Costa Rica | Limon | truck |
| 24 | 3/25/95 | Panama | Darien | canoe |
| 25 | 9/9/95 | Panama | Colon | truck |
| | 9/12/95 | Panama | Bocas del Toro | STRI *R/V* |
| 26 | 12/6/95 | Venezuela | Falcon | truck |
| | 12/11/95 | Venezuela | Araya Peninsula | truck |
| | 12/14/95 | Venezuela | Isla de Margarita | truck |
| 27 | 4/8/96 | Panama | Darien | canoe |
| 28 | 3/24/96 | Trinidad | Manzanilla | car |
| 29 | 6/29/96 | Costa Rica | Limon | truck |
| 30 | 1/5/97 | Venezuela | Falcon | truck |
| | 1/10/97 | Venezuela | Araya Peninsula | truck |
| | 1/13/97 | Venezuela | Cumana | truck |
| | 1/14/97 | Venezuela | Isla de Margarita | truck |
| 31 | 1/10/97 | Panama | Bocas del Toro | STRI *R/V* |
| 32 | 1/8/98 | Panama | Bocas del Toro | motor boat |
| | 1/16/98 | Panama | Colon | truck |
| 33 | 10/9/98 | Ecuador | Borbon | truck, canoe |
| | 10/17/98 | Ecuador | Manabi | truck |
| 34 | 6/9/99 | Ecuador | Borbon | truck, canoe |
| | 6/17/99 | Ecuador | Manabi | truck |

sults, most of which appear in this volume. The geographic scale, or spatial resolution, of the research varies with taxonomic group. At one extreme, higher-level taxa that are quite diverse and widely distributed in the Caribbean (*e.g.*, mollusks) require an enormous sampling effort for results that are meaningful at the scale of an ocean basin. At the other extreme, higher-level taxa that are less diverse and also more restricted environmentally, such as reef corals (~175 Neogene-Recent Caribbean species), require less sampling. Most taxa in this project fall between the two extremes, *e.g.*, benthic foraminifera are moderately diverse and normally distributed across the entire Caribbean (some globally), and cheilostome bryozoans are moderately diverse but more endemic.

Differences in spatial and temporal distributions of taxa studied by the PPP are reflected by the approaches to evaluating diversity. Cheetham *et al.* (Chapter 8, cheilostome bryozoans) and Jackson *et al.* (Chapter 9, mollusks) address the adequacy of PPP collections for calculating total diversity by plotting cumulative numbers of the species recovered as a function of the numbers of collections examined in each area. Whereas collections are still inadequate to determine total Caribbean molluscan generic diversity per time interval, relative molluscan diversity for successive time intervals has been compared. The cumulative curves for bryozoan species show a slight flattening which suggests that total diversity is being approached, and Cheetham *et al.* identify trends in diversity for adequately sampled growth forms of cheilostomes. Collins (Chapter 5, benthic foraminifera) and Jackson both use Fisher's alpha to measure local diversity, an approach that avoids the enormous task of calculating total regional diversity. Cairns (Chapter 6, azooxanthellate corals) combines PPP data with other data to address Caribbean species richness and evolution from Neogene to Recent time.

## AGES OF FORMATIONS EXAMINED BY THE PPP

Ages have evolved over the course of the project and continue to do so. Time scales change (Berggren *et al.*, 1985; Berggren *et al.*, 1995), new exposures that represent older or younger parts of previously dated formations are discovered, the evolutionary and paleoceanographic history of microfossils becomes better known, and resampling previously dated sections and new paleomagnetic studies sometimes result in age refinement. In this volume, biostratigraphy completed before 1993 (Bybell, Chapter 2; Cotton, Chapter 3) used an older time scale, as do most of this volume's chapters, while current biostratigraphic research (Aubry and Berggren, Appendix 1 of Chapter 1) has begun

Table 3.—Ages of Caribbean stratigraphic units examined by the PPP, based on the time scale of Berggren *et al.* (1995).

| Formation | Member/facies/section | Age (Ma) |
|---|---|---|
| Cayo Agua Formation | | 5.0–3.4 |
| Chagres Formation | | 8.6–5.3 |
| Escudo de Veraguas Formation | | 3.7–1.9 |
| Gatun Formation | Lower part | 11.8–11.4 |
| Gatun Formation | Middle part | 9.4–8.6 |
| Gatun Formation | Upper part | 9.4–8.6 |
| Moin Formation | | 2.1–1.5 |
| Moin Formation | Empalme member | 2.1–1.5 |
| Moin Formation | Lomas del Mar member | 1.9–1.5 |
| Nancy Point Formation | | 7.2–5.6 |
| Quebrada Chocolate Formation | | 3.7–2.6 |
| Quebrada Chocolate Formation | Buenos Aires member | 3.3–2.6 |
| Rio Banano Formation* | | 3.8–3.0 |
| Rio Banano Formation? | Brazo Seco section** | 5.2–4.3** |
| Shark Hole Point Formation | | 5.6–3.6 |
| Swan Cay Formation | | 1.8–0.8 |
| Tobabe Formation | | 7.2–5.3 |
| Uscari Formation | Uppermost part | 8.1–5.6 |

* Aubry and Berggren (App. 1, Chapter 1) and McNeill *et al.* (in press) include an extra section above that examined by Bybell (Chapter 2) and Cotton (Chapter 3).

** From McNeill *et al.* (in press), this age (using Sr isotopes) is highly uncertain given the absence of age-diagnostic microfossils and anomalous results of Sr ages from samples in other Limon sections.

to use the newer one. Most biostratigraphy (including microfossil zonation) based on older time scales can be transfered to newer ones, so that sample ages recorded in the PPP Database use a single time scale. Table 3 summarizes current age estimates for the stratigraphic units surveyed by the PPP, based on the time scale of Berggren *et al.* (1995).

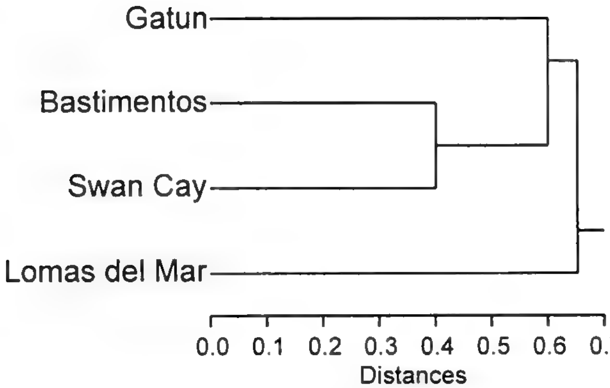
## ANALYSIS OF THE PALEOBIOTIC SURVEY DATA

The paleobiotic survey was carried out as a series of separate surveys encompassing algae, protists, invertebrates and vertebrates. The major taxa, each represented by a chapter in this book, are: calcareous nannoplankton, planktic foraminifera, benthic foraminifera, azooxanthellate corals, reef corals, cheilostome bryozoans, mollusks, ostracodes and teleost fishes. The records of nannoplankton and planktic foraminifera are not censuses of all species present because species are selectively identified from whole assemblages for biostratigraphy. For the remaining taxonomic groups, all species or genera are recorded for each site, which has a unique PPP number. In this analysis, we combine the separate censuses into one data set, conduct cluster analyses of the assemblages in stratigraphic units, and explore the relative influence of age *versus* environment, which helps in differentiating evolutionary and ecological changes.

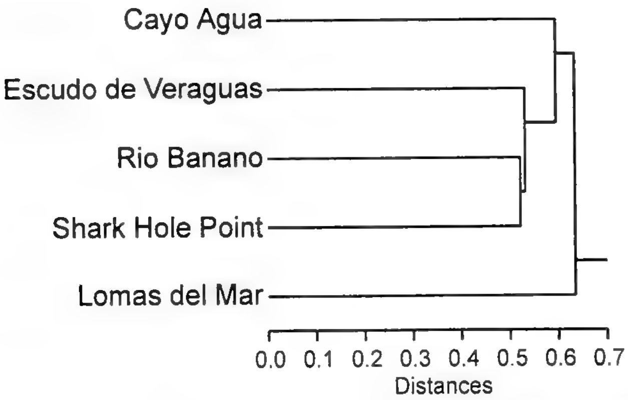
When combining paleontologists' separate data sets, all occurrence data are necessarily standardized by the coarsest sampling and recording method. Because some taxa (*e.g.*, bryozoans) are recorded only as present or absent, the other relative abundance data must be converted to presence/absence. Similarly, some taxa (*e.g.*, azooxanthellate corals) are typically sparse at individual sites or sections, so their sites are combined within each stratigraphic unit to address sampling biases. The resulting data set records the presence or absence in stratigraphic units for benthic foraminifera (333 species), azooxanthellate corals (17 species), reef corals (89 species), cheilostome bryozoans (200 species), mollusks (1022 genera to subgenera!), ostracodes (79 species) and teleost fishes (82 genera).

The eleven stratigraphic units we analyzed are the: Gatun Formation, Chagres Formation, Nancy Point Formation, Shark Hole Point Formation, Cayo Agua Formation, Fish Hole section of Bastimentos Island, Escudo de Veraguas Formation, Swan Cay Formation, Uscari Formation, Rio Banano Formation, and the Lomas del Mar Member of the Moin Formation. Nevertheless, there are missing data for taxonomic groups in many of these units. For example, reef corals are absent from most units, ostracodes are not censused in the Panama Canal Basin, and azooxanthellate corals are not yet recorded from the deeper-water units or Panama Canal Basin. Therefore, separate analyses are performed on various combinations of taxonomic groups and stratigraphic units. The cluster analyses use six different algorithms (Ward's method and single, complete, centroid, average and median linkage) with only slightly different results; a typical result is figured below for three combinations of taxa and stratigraphic units.

1. In Text-figure 1 are the results of the only analysis that includes reef corals, as well as mollusks and fish. Bastimentos and Swan Cay, both in the Bocas del Toro Basin, are the most similar, and Lomas del Mar, in the Limon Basin, is the most different. This result (which holds with or without the corals) confirms interbasinal differences noted previously (Collins *et al.*, 1995), and appears to confound predictions based on the Late Pliocene–Early Pleistocene turnovers in molluscan and reef coral taxa (Jackson *et al.*, 1993; Budd *et al.*, 1996). On the basis of age, Swan Cay and Lomas del Mar, deposited after the turnovers, should be most similar: Bastimentos is 2.6–2.4 Ma, Swan Cay is 1.8–0.8



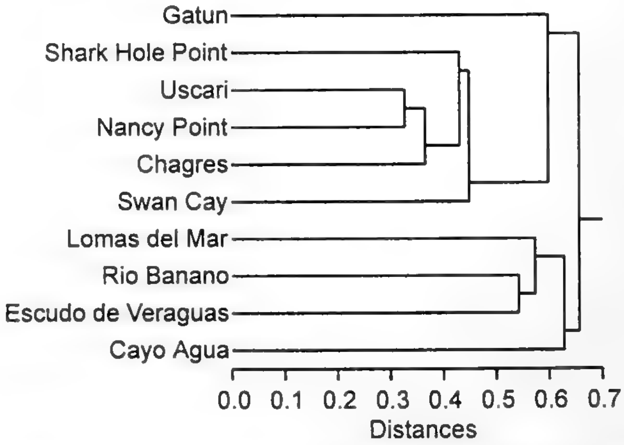
Text-figure 1.—Cluster analysis (complete linkage method) of the presence/absence of species of reef corals, genera of teleost fishes, and genera to subgenera of mollusks in the Gatun Formation (Panama Canal Basin), the Fish Hole section of Bastimentos Island (Bocas del Toro Basin), the Swan Cay Formation (Bocas del Toro Basin), and the Lomas del Mar Member of the Moin Formation (Limon Basin). Distances are Euclidean. Assemblages from the same basin are more similar than assemblages from the same age or bathymetry.



Text-figure 2.—Cluster analysis (complete linkage method) of the presence/absence of taxa in the Cayo Agua, Escudo de Veraguas, and Shark Hole Point formations of the Bocas del Toro Basin, and the Rio Banano Formation and Lomas del Mar Member of the Moin Formation in the Limon Basin. Included in the analysis are species of benthic foraminifera, azooxanthellate corals, cheilostome bryozoans, and ostracodes, genera of teleost fishes, and genera to subgenera of mollusks. Distances are Euclidean. Age and environment have approximately equal influences on the similarity of assemblages.

Ma, and Lomas del Mar is 1.9–1.5 Ma. Units do not cluster by paleobathymetry, either: Bastimentos and Lomas del Mar are middle neritic, and Swan Cay is shallowest outer neritic with transported middle neritic material.

2. Text-figure 2 shows the similarity of five stratigraphic units using all taxa except reef corals. Age and environment affect the similarity of the units' faunal assemblages about equally. Although the Rio Banano and Cayo Agua formations are most alike in environment (inner-middle neritic), the former is linked first to an outer neritic unit of a comparable, Early-middle Pliocene age, the Shark Hole Point Formation. However, the Escudo de Veraguas Formation, which is Late Pliocene and mixed middle to outer neritic, is most similar to the first two units, suggesting that environment has a stronger influence in this grouping than age. The unit that is most different in both environment and age, the reefal, latest Pliocene to earliest Pleistocene Lomas del Mar Member, has the most different faunal assemblage.
3. Text-figure 3 is an analysis of ten stratigraphic units using only benthic foraminifera, fish and mollusks. It suggests that environment influences the similarity of assemblages more than age, although age and environment are somewhat correlated because of the progressive Neogene uplift of the Bocas del Toro and Limon basins. There are two main clusters. In the upper one, the Late Miocene, bathyal Uscari, Nancy Point and Chagres formations are most similar. The next shallowest units, the outer neritic, Early Pliocene and Pleistocene Shark Hole Point and Swan Cay formations, are most similar to the bathyal units. The older, shallower Gatun Formation falls between the old, deep units in the upper cluster and the lower cluster of shallower-water, Pliocene–earliest Pleistocene units.



Text-figure 3.—Cluster analysis (complete linkage method) of the presence/absence of taxa in the Gatun and Chagres formations of the Panama Canal Basin; the Shark Hole Point, Nancy Point, Swan Cay, Escudo de Veraguas, and Cayo Agua formations of the Bocas del Toro Basin; and the Uscari Formation, Lomas del Mar Member of the Moin Formation, and Rio Banano Formation of the Limon Basin. Included in the analysis are species of benthic foraminifera, genera of teleost fishes, and genera to subgenera of mollusks. Distances are Euclidean. Environment seems to influence the similarity of assemblages more than age.

We conclude from these exploratory analyses that there are strong age, paleoenvironment, and basin effects on the similarity of PPP assemblages. Age reflects evolutionary changes but is somewhat correlated with paleoenvironment because of regional tectonic uplift through time. Similarities of assemblages from the same paleoenvironments result from ecological associations, and the basinal effect reflects more localized conditions. Analyses of this sort begin to disentangle evolutionary and ecological faunal changes for the ultimate purpose of isolating evolutionary events. These analyses are of multiple, higher-level taxa recorded as presence/absence in stratigraphic units, and future analyses using relative abundances and a finer-scaled chronology will undoubtedly reveal other trends in evolution and ecology.

## CONTENT OF CHAPTERS

The volume is divided into two parts. Part 1, Stratigraphy and Paleoenvironment, consists of four chapters on the formal lithostratigraphy, biostratigraphy, geochronology, and paleoenvironments of sediments from the Panama Canal, Bocas del Toro, and Limon basins. The chapters are summarized as follows:

Chapter 1. Coates places the physical stratigraphy of Neogene sediments of Caribbean Panama and Costa Rica within a regional tectonic framework, incorporating the units defined in Coates *et al.* (1992) and creating several new ones. In Appendix 1 of Chapter 1, Aubry and Berggren give the latest biostratigraphic data and chronological correlation of the new sections.

Chapter 2. Bybell presents calcareous nannofossil data collected until 1991, and discusses their application to the geochronology of the formations described by Coates *et al.* (1992). Her research laid the foundation upon which the later biochronology was built.

Chapter 3. Cotton presents data from planktic foraminifera collected before 1993 and combines it with the nannofossil data for refined age estimates of formations. He correlates the Central American formations with other tropical to subtropical American formations from southeastern Virginia to Ecuador.

Chapter 4. Collins, Aguilera, Borne and Cairns combine environmental assignments from four different phyla (benthic foraminifera, teleost fishes, ostracodes, and ahermatypic corals, respectively) for most stratigraphic units. The results among taxa are remarkably congruent, considering the different life modes of the organisms (*e.g.*, benthic *versus* nektonic; feeding at *versus* above the subtratum), as well as variations in technical and analytical approach. The paleoenvironments for individual sections are combined for an overview of larger-scale environmental change set within the region's tectonic history.

Part 2, Paleobiotic Survey, includes seven chapters that report the distribution of species or genera at PPP sites, and address topics such as faunal and paleoenvironmental change through time. Some of the conclusions of Chapters 5 to 12 are summarized as follows:

Chapter 5. Collins combines fossil and modern distributions of species of Caribbean benthic foraminifera from Panama and Costa Rica and shows that their diversity has doubled from the Late Miocene to Recent, through the time of seaway constriction, complete closure, and afterward. The proportion of taxa associated with carbonate shoals and reefs increased during this time, which agrees with the trend of increasing speciation in these ecologically restricted taxa. The largest faunal changes apparently occurred in the Pleistocene to Recent rather than the middle Pliocene, suggesting that complete seaway closure had little effect.

Chapter 6. Cairns reports the stratigraphic ranges of 142 Caribbean azooxanthellate coral species, 101 of which are extant. The data suggest that the highest origination rate occurred in the Middle to Late Miocene and the highest extinction rate occurred in the Late Pliocene. Neither of these evolutionary pulses occurred near the time of complete seaway closure.

Chapter 7. Budd, Johnson, Stemann, and Tompkins describe the distribution of reef coral species from the Limon Basin, and identify different periods of faunal change that occurred at various Caribbean localities during the Late Pliocene to Pleistocene.

Chapter 8. Cheetham, Jackson, Sanner, and Ventocilla contrast assemblages of cheilostome bryozoans from both sides of the Central American isthmus with those of the Dominican Republic in an analytical comparison of Caribbean and Pacific faunas. An unexpected result is that the complete closure of the isthmian seaway apparently had relatively little evolutionary effect. The authors also find a Middle Miocene to Pleistocene decline in the diversity of erect species, possibly associated with their growth on decreasingly available substrata such as seagrass.

Chapter 9. Jackson, Todd, Fortunato and Jung control for sampling and taxonomic biases in an enormous dataset of Neogene molluscan genera to subgenera from Caribbean Panama and Costa Rica. Local molluscan diversity varied more than six-fold, and either increased or remained constant from the Miocene to Recent. Previous studies which identified a decline in Pliocene Caribbean molluscan diversity and associated it with seaway closure were based on inadequate sampling of the faunas.

Chapter 10. Borne, Cronin and Hazel use assemblages of ostracodes from the Limon and Bocas del Toro basins to identify lagoon, carbonate platform, restricted nearshore, and outer shelf to upper slope facies. The distributions and morphology of several species suggest that cold, upwelling currents impinged on the Late Pliocene to Early Pleistocene Central American shelf.

Chapter 11. Aguilera and Aguilera describe teleost fish assemblages at the genus level from otoliths, and infer bathymetries by comparison to living representatives of the genera. Several genera, found living only in the Indo- or Western Pacific, show that relict elements of Tethyan faunas persisted in the Caribbean until at least the Late Pliocene.

Chapter 12. Kaufmann presents a data model that explains the way in which the elements of the PPP function as a whole, as well as the working of the database of information on stratigraphy, geography, chronology, paleoenvironment, and faunal occurrence. For complex projects, data models help clarify the relationships of the many, diverse parts.

Appendices. Coates locates all PPP collecting sites used in this volume, plotting them on maps in Appendix A. Each site is represented by a unique PPP number. In Appendix B, he places the sites stratigraphically in a series of 39 detailed sections.

## SUMMARY

For the Panama Paleontology Project, the whole is much greater than the sum of the parts. Basing studies of multiple, higher-level taxa on the same, well-dated set of samples has provided many possibilities for integrated research. A few of the conclusions the PPP can make thus far, based on the Caribbean collections, are the following:

1. *Stratigraphy.* There exists along the Caribbean coast of Panama and Costa Rica a series of exposures of richly fossiliferous, Neogene, shallow-water sediments which, when placed in stratigraphic succession, cover the late Middle Miocene to Early Pleistocene interval.
2. *Chronology.* The fossil collections can be dated biostratigraphically and paleomagnetically with a precision that is relatively fine for land-based formations, with age ranges for single samples varying between approximately 100,000 years and 1.5 million years.
3. *Environments.* The Panama Canal Basin was a shallow Middle Miocene basin until deepening ~6 Ma caused an inflow of deep, Pacific water. The Bocas del Toro and Limon basins differed in sediment source, isobathyal microfaunas, and stable isotopes. They were similar in their back-arc setting, histories of uplift, and sedimentary sequences of bathyal Miocene mudstones, neritic Pliocene siltstones/sandstones, and lower Pleistocene coral reefs.
4. *Seaway closure.* To date, research on PPP collections shows no strong evolutionary response to the complete closure ~3.5 Ma of the Central American isthmian seaway, although an evolutionary turnover in reef corals did occur sometime between 4 and 1 Ma. Whereas the largest pulses of origination in the Neogene occurred for azooxanthellate corals and benthic foraminifera in the Middle and Late Miocene, during seaway constriction, they occurred in the latest Pliocene to Early Pleistocene for the mollusks, perhaps because of increased northern hemisphere glaciation. Complete seaway closure apparently had relatively little evolutionary effect on cheilostome bryozoans.
5. *Biodiversity.* From Late Miocene to Recent time, the diversity of molluscan genera either increased or remained constant and that of species of benthic foraminifera increased. From the Middle Miocene to the Pleistocene, the diversity of erect cheilostome bryozoans declined.

## ACKNOWLEDGMENTS

Grants from the Biotic Surveys and Inventories Program of the National Science Foundation (grant numbers BSR90-06523, DEB-9300905, DEB-9696123, DEB-9705289) provided the means to build the PPP Database, prepare large numbers of samples, track fossil collections, and assign ages and paleoenvironments. The National Geographic Society has consistently funded PPP fieldwork in Panama, Costa Rica, Nicaragua and Ecuador. The Smithsonian Institution, STRI, Swiss National Science Foundation, and Naturhistorisches Museum Basel have also funded fieldwork and the preparation of collections. This is contribution number 10 to The Program in Tropical Biology at Florida International University.

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# PART 1

# STRATIGRAPHY AND PALEOENVIRONMENT

# CHAPTER 1

## LITHOSTRATIGRAPHY OF THE NEOGENE STRATA OF THE CARIBBEAN COAST FROM LIMON, COSTA RICA, TO COLON, PANAMA

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## INTRODUCTION

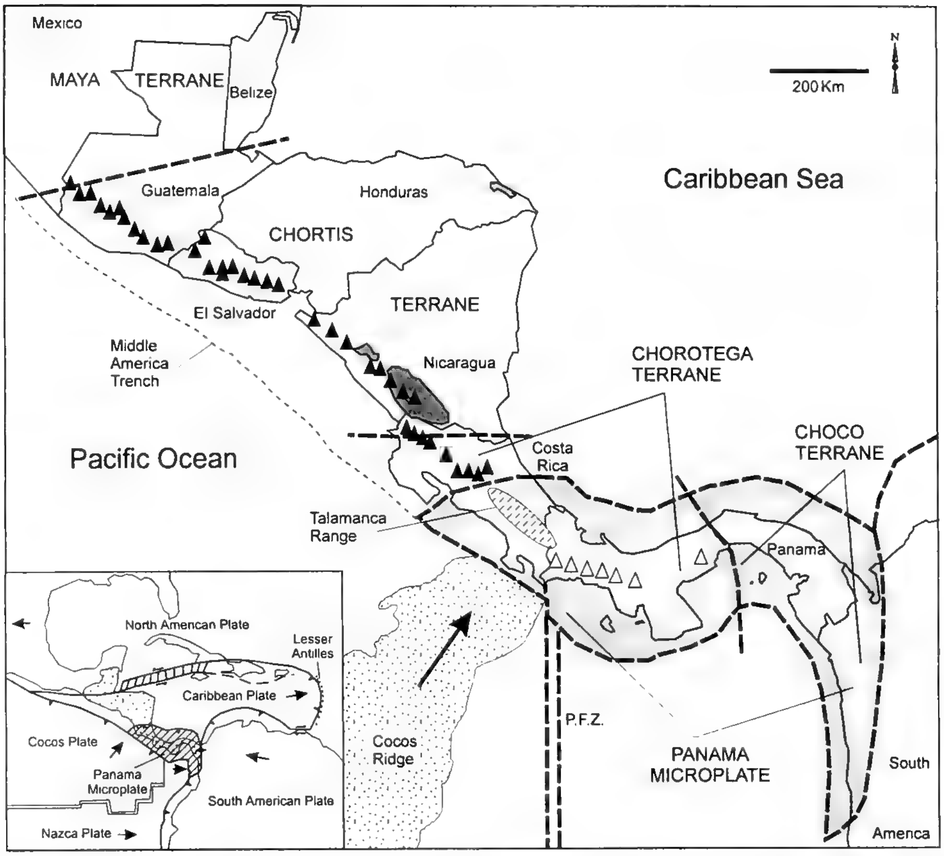
The Central American isthmus lies at the intersection of six tectonic plates (Text-fig. 1; Burke *et al.*, 1984; Mann *et al.*, 1990). The North and South American Plates, with relative westerly and west-northwesterly motions, respectively, override two large oceanic Pacific plates, the Cocos and Nazca, with northeasterly or easterly relative motions, respectively. The collision of these two sets of plates has formed, since the Cretaceous, a major zone of subduction along the western margin of the Americas, a segment of which constitutes the Central American volcanic arc.

The southern Central American isthmus consists primarily of igneous and sedimentary rocks of oceanic crustal composition, generated by the Central American volcanic arc. In this chapter, I focus on the stratigraphy of three important sedimentary basins that flank the magmatic arc on the Caribbean side (Text-fig. 2), namely, the southern Limon Basin in Costa Rica, and the Bocas del Toro and Panama Canal basins in Panama. These basins are dominated by volcaniclastic sediments, commonly with foraminiferal and nannofossil microfaunas. They also contain important Miocene through Pleistocene coral reefs, as well as a series of rich and diverse molluscan, bryozoan, fish (otoliths), and coral assemblages at many stratigraphic levels. In this chapter, I present a revision of the formal stratigraphy of the sediments in which the faunas occur, including the definition of several new formations and their biochronology (Appendix 1 this chapter). Also included are 11 maps and detailed insets, showing the location of all samples (Appendix A, this volume), and the computer-drawn logs of 39 sections measured across the three basins that show the stratigraphic relations of all the samples (Appendix B, this volume). The locations of the measured sections are shown in Text-figure 2.

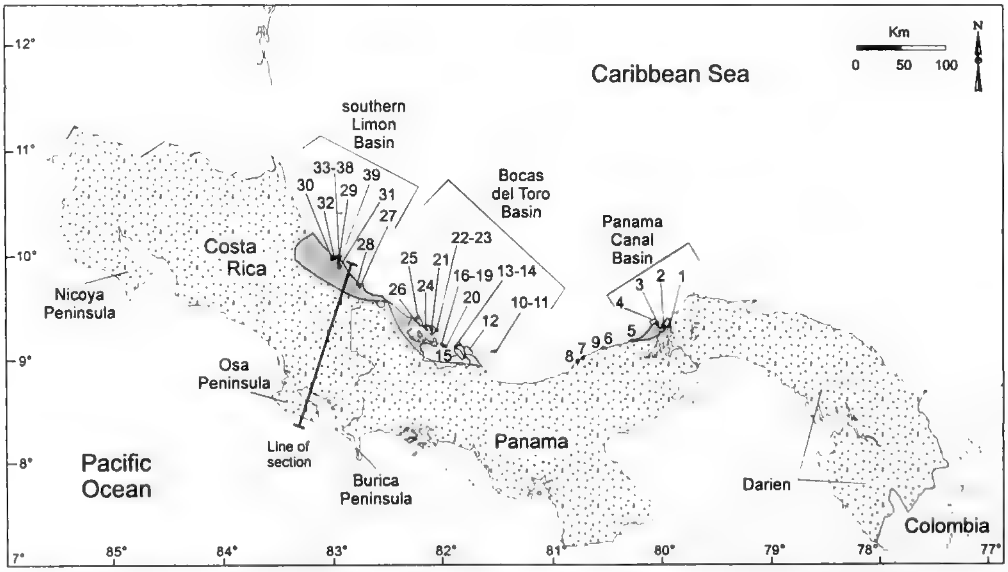
The Isthmus of Panama was the last portion of the Central American isthmus to emerge (Coates *et al.*, 1992; Coates and Obando, 1996), closing the marine connections between the Caribbean and the Pacific about 3 Ma (Kaneps, 1970; Berggren and Hollister, 1973, 1974; Keigwin, 1978, 1982). The Panama Paleontology Project (PPP) set out to look for extensive upper Neogene fossiliferous sedimentary sequences in this region on the assumption that the sedimentary record here would track most closely the marine environmental and ecological changes caused by the emergence of the Isthmus.

The stratigraphic sections and faunal samples analyzed in this volume are located in back-arc basins (*e.g.*, southern Limon Basin) or in marginal aprons (*e.g.*, Bocas del Toro and Panama Canal Basins) derived from the Caribbean side of the Central American volcanic arc, the structure of which is shown in cross section in Text-figure 3. Although we originally undertook field expeditions to both Pacific fore-arc and Caribbean back-arc basins, the Caribbean sequences yielded more complete stratigraphic sections and more abundant and diverse faunal assemblages. This is largely due to erosion of many younger sequences on the tectonically active Pacific coast. Older sediments have been subducted or obducted onto the overlying plate and are either highly deformed or lost (Text-fig. 3). By contrast, on the passive Caribbean margin, the southern Limon, Bocas del Toro, and Panama Canal basins (Text-fig. 2) have yielded numerous diverse and abundant faunas. These sections are less deformed, and span a greater time interval than the Pacific sections. For example, the Pacific Burica Peninsula fore-arc basin (Corrigan *et al.*, 1990; Coates *et al.*, 1992) has more than 4000 m of sediments, ranging from about 3.5 to <1.6 Ma, whereas the Caribbean Bocas del Toro Group has about 1000 m, ranging from 8.5 to about 1.5 Ma. In the region of the Talamanca Range (Text-fig. 1) in Costa Rica, subduction of the Cocos Ridge has elevated and structurally deformed both the inner fore-arc Terraba Basin and the now inverted back-arc southern Limon Basin (Kolarsky *et al.*, 1995), as is shown in Text-figure 3.

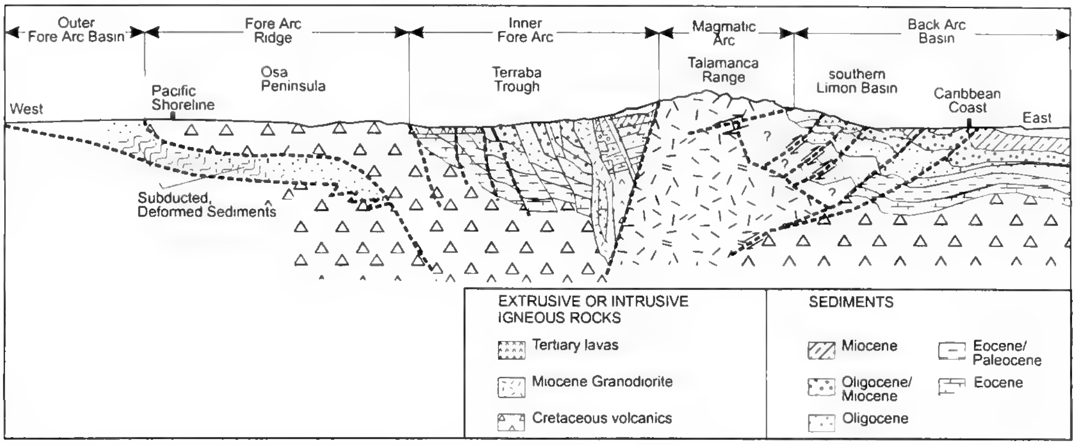
From 1986 to 1992, the PPP undertook a series of reconnaissance field expeditions to explore a number



Text-figure 1.—Map of Central America showing location of the older Maya, Chortis, Chorotega, and Choco geological terranes, and the younger Panama microplate, picked out in thick dashed lines and gray stipple. The northern border of the Panama Microplate is called the North Panama Deformed Belt. Also shown is the Talamanca Range (dash-dot stipple) and the volcanoes of the central magmatic arc (black triangles = active, open triangles = inactive).



Text-figure 2.—Map of Costa Rica and Panama showing location of the southern Limon, Bocas del Toro, and Panama Canal Basins (dark gray stipple). Numbers correspond to sections referred to in text and in Appendix B.



Text-figure 3.—Schematic geologic cross section from the Osa Peninsula on the Pacific coast to the southern Limon Basin on the Caribbean coast (see line on Text-fig. 2). Modified from "Hydrocarbon potential of Costa Rica", Ministry of Environment and Energy, Government of Costa Rica, 1996.

of the Neogene sedimentary fore- and back-arc basins associated with the volcanic arc in southern Central America. Basins were surveyed on the Pacific coast, from the Nicoya Peninsula, northwestern Costa Rica, to Darien, eastern Panama, and on the Caribbean coast, from the northern part of the Limon Basin, Costa Rica, to the Panama Canal Basin, Panama (Text-fig. 2). In a preliminary review of the litho- and bio-stratigraphy, Coates *et al.* (1992) established that a well-preserved and diverse marine fossil record existed on both coasts, containing nannofossils and planktic foraminifera capable of yielding a precise geochronology for the late Neogene sediments.

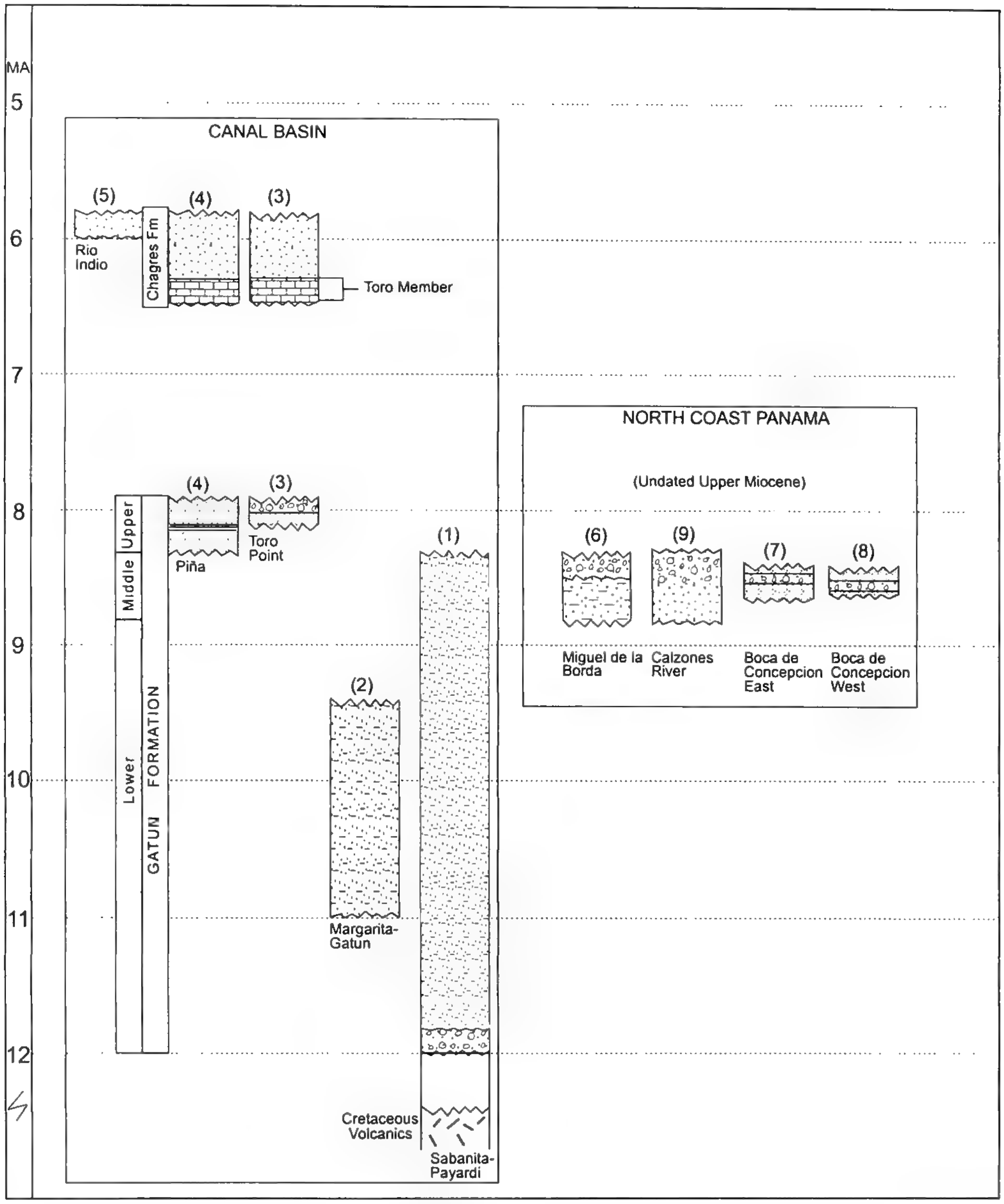
In 1993, with a view to more detailed comparisons of geologic history and evolutionary and ecological patterns, the PPP began a more extensive series of field expeditions. These focused particularly on the complete and richly fossiliferous sections of the Caribbean coast, specifically in the southern Limon, Bocas del Toro, and Panama Canal basins (Text-fig. 2) described here. The northern part of the Limon Basin is not treated in this chapter because it is extensively covered by Pleistocene volcanic deposits and did not yield abundantly fossiliferous sections.

Because the Miocene to Pleistocene sediments of the southern Limon Basin are relatively elevated and structurally complex, the physical stratigraphy of this basin has been difficult to reconstruct (Text-fig. 3). The stratigraphic sequence has been studied mostly along rivers draining the foothills and coastal plain northeast of the Talamanca Range in the area around Limon (Map 11) and, to a lesser extent, further south as far as the Panamanian border (Map 10). Many new, extensive and very fossiliferous Plio-Pleistocene sections were exposed during our field work, often only temporarily, by housing construction in the hills of the western part of Limon and by commercial construction along Route 32 between Buenos Aires and Limon (Insets A, B, Map 11).

In contrast to the sediments of the southern Limon Basin, the Miocene to Pleistocene deposits of the Bocas del Toro Basin are mostly exposed along the coast, and are generally only gently folded. In the Bocas del Toro Basin (Text-fig. 2), flat-lying sediments are extensively exposed along coastal sections of the islands and peninsulas of the archipelago. Access to these sections is by sea and many can only be studied in relatively calm weather. Geological mapping and section measuring were done using a 22-foot boat, but large-scale bulk fossil sampling was carried out by PPP expeditions of 6 to 12 persons using the research vessels *Benjamin* and *Urraca* of the Smithsonian Tropical Research Institute.

The Upper Miocene Panama Canal Basin (Text-fig. 2) sediments are observed in roadside exposures from Sabanita to Colon, and in coastal exposures from Colon to Gobea, about 40 km to the west. (Map 1). The Gatun Formation was studied in numerous, often temporary, construction sites along or near Route 3, between Sabanita and Colon, along the road to the Payardi Oil Refinery, between Gatun and Margarita, and around the Gatun Dam (Map 1). Also included in this study are a few localities at the mouths of rivers along the north coast of Panama, between the Valiente Peninsula, Bocas del Toro, and Gobea (Maps 2,3).

The following account of the lithostratigraphy of the southern Limon, Bocas del Toro, and Panama Canal basins revises that of Coates *et al.* (1992) and Bottazzi *et al.* (1994), adding new information obtained in subsequent field work, including new formal stratigraphic



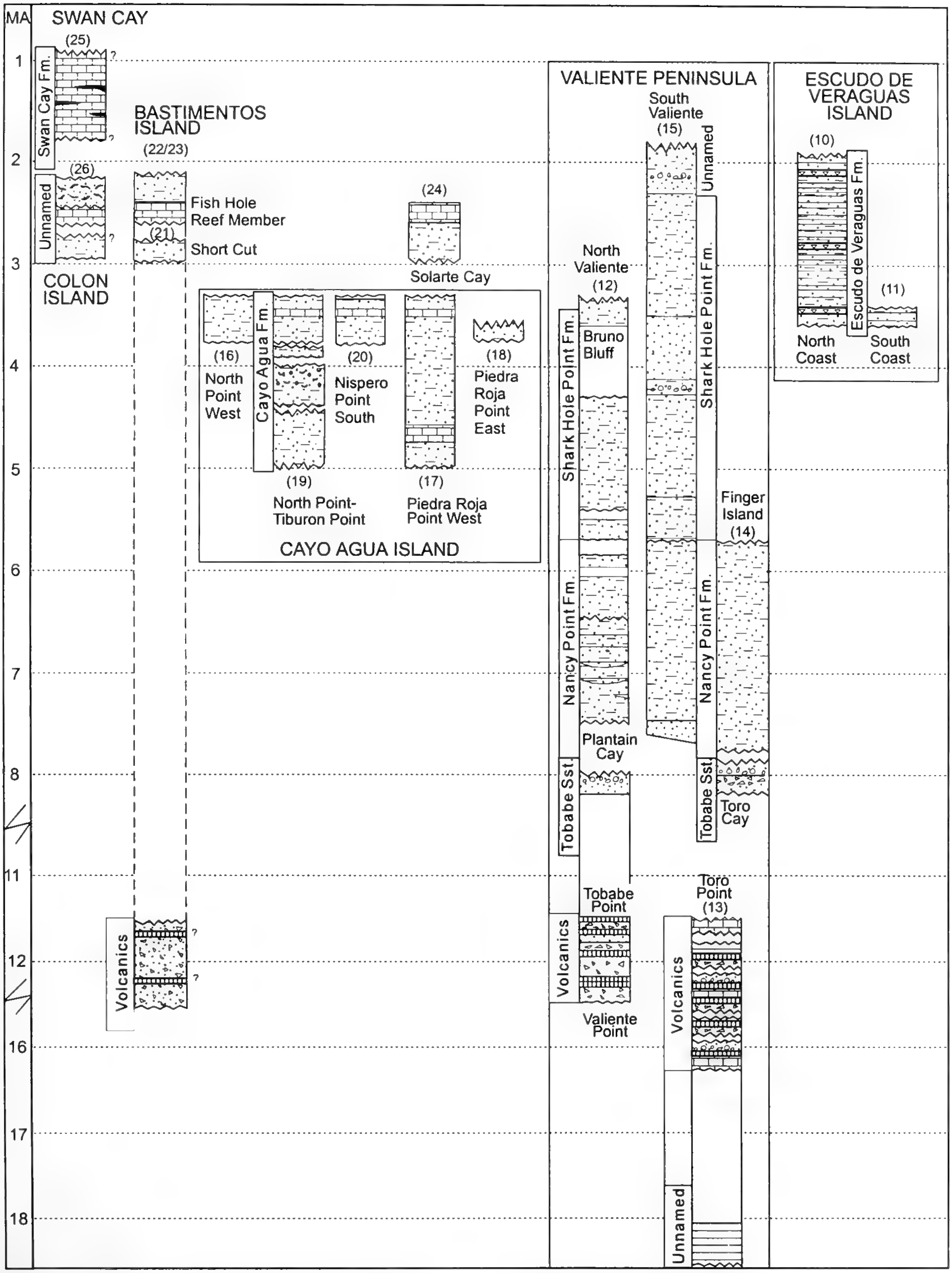
Text-figure 4.—Correlation of measured sections from the Panama Canal Basin and along the north coast of Panama. Numbers in parentheses refer to sections in Appendix B, this volume. Lithologic patterns correspond to the lithologic key in Appendix B.

units. The temporal range and formal nomenclature of the stratigraphic sequences in the three basins are summarized in Text-figures 4, 5, and 6. The bases for the age assignments are discussed by Aubry and Berggren Appendix 1, (this chapter).

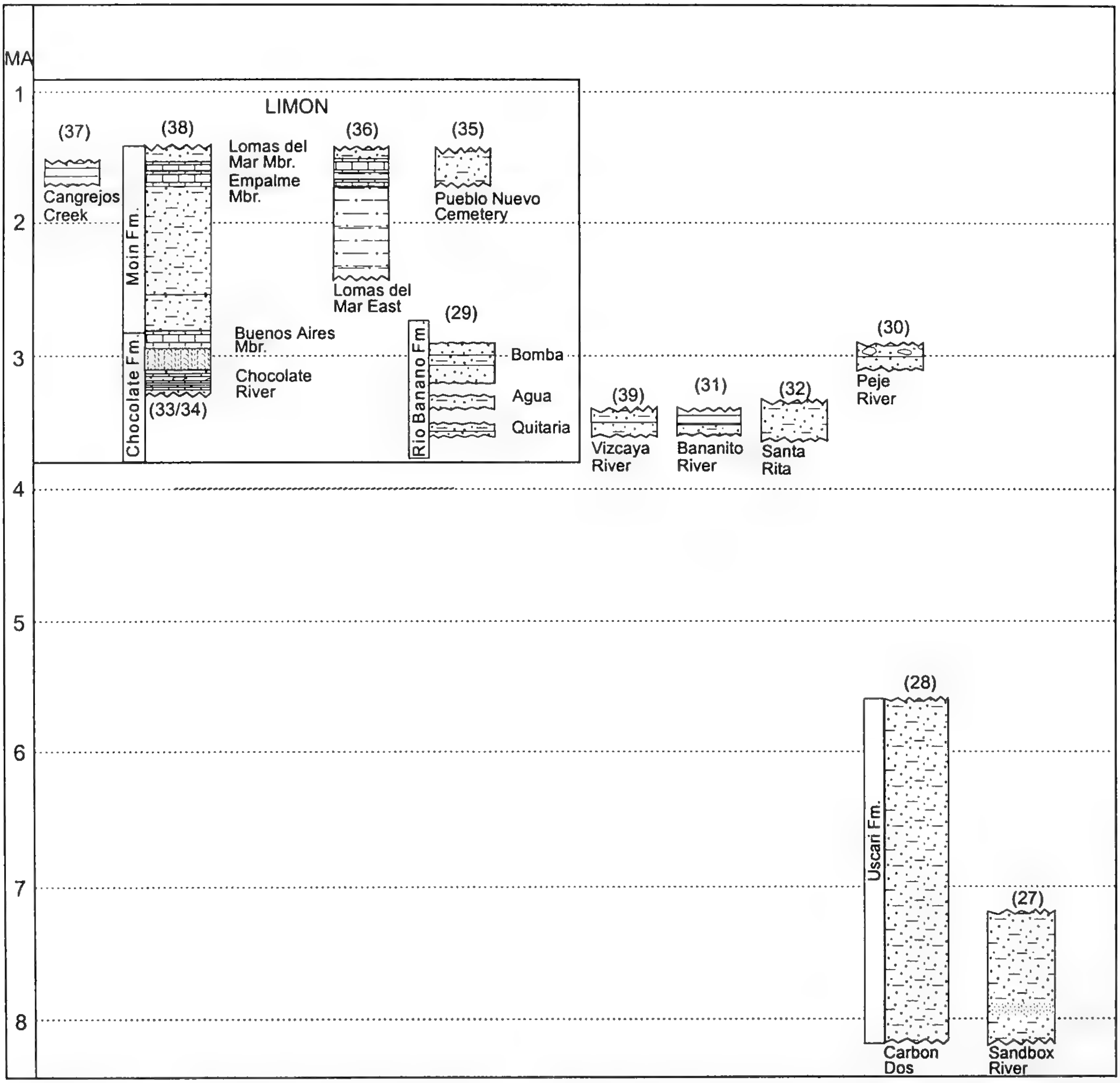
Five stratigraphic sections were measured in the Panama Canal Basin: 4 along the north coast of Panama, 17 in the Bocas del Toro Basin, and 13 in the Limon Basin (Appendix B, this volume). Fossil collections are located by their PPP number on the maps in Appendix A, (this volume), and stratigraphically on each section in Appendix B, (this volume). These PPP numbers also link all files in the PPP Database (Kaufmann, this volume) which is also available at the internet site http://www.fiu.edu/~collinsl/. Currently, a paleomagnetic sampling project is being completed on the stratotypes of the Limon (McNeill *et al.*, in press) and Bocas del Toro groups that will be integrated with the litho- and biostratigraphy to refine the geochronology.

## ACKNOWLEDGMENTS

Many people have helped me in the field since the PPP started in 1986. Jeremy Jackson, Laurie Collins, Peter Jung, and Ann Budd, my colleagues on the Steering Committee of the PPP, have been my most



Text-figure 5.—Correlation of measured sections in the Bocas del Toro Basin. Numbers in parentheses refer to sections in Appendix B, this volume. Lithologic patterns as for Text-figure 4.



Text-figure 6.—Correlation of measured sections in the southern Limon Basin. Numbers in parentheses refer to sections in Appendix B, this volume. Lithologic patterns as for Text-figure 4.

constant field companions. Marie-Pierre Aubry, Bill Berggren, and Don McNeill, identifying calcareous nannofossils, planktic foraminifera, and taking and processing paleomagnetic samples, respectively, have also spent much time in the field and even more in the laboratory, integrating the litho-, bio-, and magnetostratigraphy. To them all I owe a special debt of gratitude. I thank Dana Geary, Tom Cronin, Susan Kidwell, John Sutter, Claudia Johnson, Erle Kauffman, Simon Mitchell, Orangel Aguilera, Jorge Obando, and Jon Todd, all of whom provided valuable insights into field interpretations on various occasions. Valuable assistance in measuring sections and collecting samples was also provided by Laurie Andersen, Mairi Best, Pam Borne, John-Mark Coates, Tim Collins, Mat Cotton, Helena Fortunato, Antoine Herz, Ken Johnson, Rene Panchaud, Stephen Rhodes, Jay Schneider and Tom Stemann. My thanks are also due to Sebastian Castillo, who guided my boat for many years, and to Beatrice and Lucien Ferrenbach for constant logistical help and wonderful hospitality throughout this project. I am also very grateful for very helpful reviews from Paul Mann and Joe Hartman. This chapter could not have been completed without the extraordinary contribution of my research assistant Xenia Guerra. She is responsible for the locality maps and the conversion of my field notes into computer-drawn sections that comprise Appendices A and B, and for drawing all the text-figures. She undertook the task of checking that 2531 samples were properly recorded on all sections and maps. She has accompanied me in the field to process samples, edited the manuscript, and ensured that I was always equipped with the appropriate field maps, for all of which I am especially grateful. Lastly, my profound thanks to Janet Coates, my wife, who acted as my field assistant on numerous occasions, tolerated long absences on other occasions, helped organize many expeditions, and generally supported PPP activities in so many ways.

## GEOLOGICAL SETTING

The Central American isthmus forms the western margin of the Caribbean and lies at the center of a complex intersection of the Pacific, Cocos, and Nazca plates with the Caribbean Plate and the small Panama Microplate (Text-fig. 1). The dominantly oceanic Caribbean Plate lies between the North and South American plates. Its relative eastward motion, with respect to the North and South American plates is accommodated by strike-slip faults to the north and in part to the south (but now confounded by compression from the west-northwestward-moving South American Plate). In the east, it is bounded by the subduction zone of the Lesser Antilles. The western margin of the Caribbean Plate is more complex; in the northern part of the western margin, the Cocos Plate is in contact with the Caribbean Plate. In the southern portion of the western margin, a triple junction brings the Cocos and Nazca Plates in contact with the small Panama Microplate (Text-fig. 1). The Panama Microplate appears to have formed by northward escape from compression of the South American and Cocos/Nazca plates, which created its northern border, the North Panama Deformed Belt. Much of Central America lies either on the trailing western edge of the Caribbean Plate or on the Panama Microplate but a portion lies on the southwestern corner of the North American Plate (Text-fig. 1).

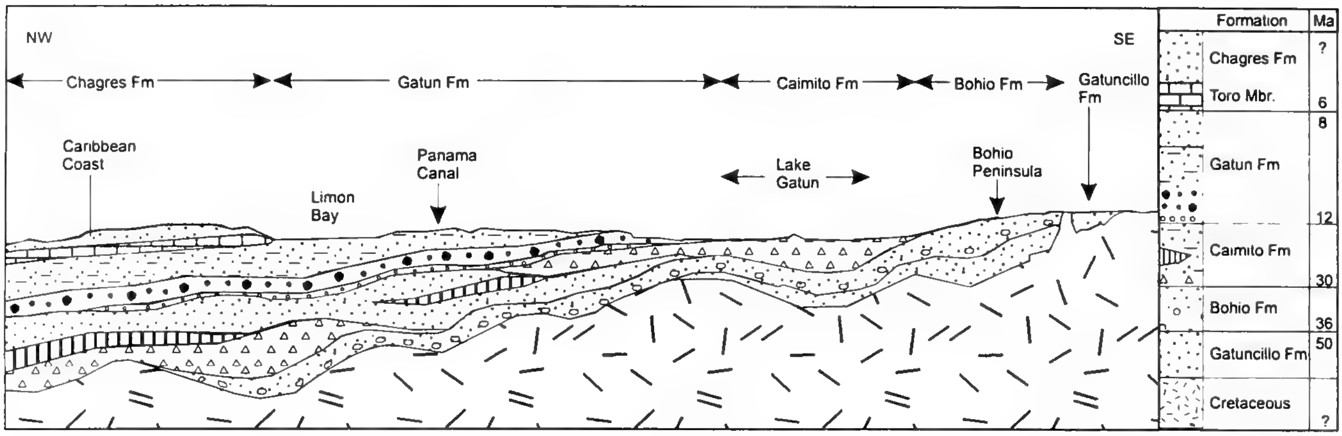
Since their formation in the Miocene, the two Pacific plates have impinged on Central America with different motions. The Cocos Plate, with relative northeasterly motion, is subducting vigorously under Central America as far south as the Costa Rica-Panama border so that this region is a zone of active volcanism and seismicity. In contrast, the Nazca and Panama Microplate border south of Panama, is relatively aseismic and without active volcanoes (Text-fig. 1). The oceanic crust of the Panama Microplate is typical of the widespread basalt plateau that underlies much of the rest of the Caribbean Plate (Burke, 1988; Burke *et al.*, 1978; Case *et al.*, 1990). This is in striking contrast to northern Central America, where much of the crust is older continental material (Donnelly *et al.*, 1990). Younger volcanic deposits are found only along the western margin of the isthmus adjacent to the volcanic arc associated with the subduction of the Cocos Plate.

Northern Central America consists of 1) the Maya Terrane, underlying Chiapas and Yucatan in southern Mexico, Belize, and Guatemala north of the Motagua River; and 2) the Chortis Terrane, which forms the rest of Guatemala, El Salvador, Honduras, and Nicaragua (Text-fig. 1). In the Maya and Chortis terranes, the isthmus is broad, formed of continental crust, and has a geologic history extending back to the early Paleozoic. For reviews of the geological history of northern Central America, see Dengo (1985), Donnelly (1992), Donnelly *et al.* (1990), Coates (1997), and references therein.

Southern Central America, the focus of this book, includes the Panama Microplate (see papers in Mann, 1995, for recent reviews), which encompasses most of Costa Rica and Panama but also includes part of northwestern Colombia (Text-fig. 1). The geology of northwestern Colombia has been reviewed by Duque-Caro (1990a, b), and the rest of the region by Escalante (1990), Mann (1995), Seyfried and Hellmann (1994), and Coates and Obando (1996).

Three major tectonic movements dominated the late Neogene tectonic evolution of the southern Central American isthmus (Kolarsky *et al.*, 1995; Coates and Obando, 1996). The first was convergent tectonics of the eastern Pacific subduction zone, the primary driving force creating the southern isthmus by forming a volcanic arc with associated fore- and back-arc basins (Astorga *et al.*, 1991). During the Miocene the arc manifested itself as an extensive archipelago stretching to South America.

The second tectonic movement, initiated about 4–3 Ma, was the shallow subduction of the Cocos Ridge, a lighter and relatively thick welt of oceanic crust trailing from the Cocos hot spot (Meschede, oral commun., 1998). This hard-to-subduct ridge rapidly elevated the Talamanca Range in particular (Text-fig. 1), and the southern isthmus in general (de Boer *et al.*, 1988; Corrigan *et al.*, 1990; Collins *et al.*, 1995; Kolarsky *et al.*, 1995). The elevation of the Talamanca Range probably



Text-figure 7.—Schematic geologic cross section of the Panama Canal Basin from the Bohio Peninsula to the Caribbean coast west of Toro Point.

also substantially reduced the number of marine connections between the Pacific and Caribbean.

The third tectonic influence on southern Central America was the convergence of the South American and Caribbean plates (Text-fig. 1), which increasingly compressed the southern Caribbean Plate margin throughout the Neogene (Silver *et al.,* 1990; Kellogg and Vega, 1995; Mann and Kolarsky, 1995). This uplifted eastern Panama and the outer Andes of northwestern Colombia and, at about 3 Ma (Keigwin, 1982), finally severed all marine connections between the Pacific and Caribbean.

## LITHOSTRATIGRAPHY

### THE PANAMA CANAL BASIN

The Panama Canal Basin (Text-fig. 2) is located at the junction of the Chorotega and Choco terranes (Dengo, 1985; Escalante, 1990), which is manifested by a major contrast in gravity (Case, 1974) and a series of north-south basement faults (de Boer *et al.,* 1988; Mann and Corrigan, 1990; Mann and Kolarsky, 1995). The stratigraphy of the complex series of laterally varying Cenozoic deposits across the Panama Canal Basin is well known because many were excellently exposed during the construction of the Panama Canal. Reviews of the Cenozoic sequence were given by Woodring (1957, 1970, 1977, 1982) and Escalante (1990). In this chapter, I am concerned only with the Neogene Gatun and Chagres formations. These two formations crop out only at the northern end of the Panama Canal Basin, along the Caribbean coast, immediately to the west and east of Colon (Map 1), and their stratigraphic relations are shown in Text-figure 7.

Collins *et al.* (1996) provided strong evidence to suggest that the southern Central American archipelago was an almost complete ecological barrier between the Pacific and the Caribbean, at the time of the deposition of the Gatun Formation (Late Miocene, about 8 Ma). The elongated outcrop pattern (Text-fig. 2), parallel to the isthmus, and the shallow marine depositional environment (20–40 m, Collins *et al.,* this volume) indicates that the Gatun Formation sediments formed as an apron of volcaniclastics flanking the isthmian arc with no marine connection to the Pacific side. However, Collins *et al.* (1996) also show that the Panama Canal Basin became temporarily a marine strait again, at about 6 Ma, during the time of deposition of the Chagres Formation, because it contains abundant bathyal benthic foraminifera of dominantly Pacific affinity.

### The Gatun Formation

*Origin of the name.*—The Gatun Formation was named by Howe (1907) after the village of Gatun which lies at the northern margin of Gatun Lake, 12 km southwest of Colon (Map 1). This name has come to supersede other earlier names for this unit, such as Monkey Hill and Mindi Beds (Hill, 1898).

*Location of stratotype.*—Section 1 includes the stratotype of the Gatun Formation defined by Coates *et al.* (1992). It runs from Sabanita on the main transisthmian highway 12 km east of Colon, to 0.7 km west of the junction with Route 77 (the turnoff for Portobelo).

*Reference sections.*—Four reference sections have been measured (Sections 2–5) that include both the Gatun and the Chagres formations and reflect the lateral changes that the formations undergo from Gobea, 40 km west of Colon, to Sabanita, 12 km east of Colon (Map 1).

*Stratal relations.*—The Gatun Formation rests unconformably on formations of different ages in different parts of the Panama Canal Basin. To the east of Colon, the Gatun Formation rests nonconformably on the unnamed Cretaceous volcanics (Text-fig. 4). To the west of Colon, including several islands in Lake Gatun, the Gatun Formation rests with angular unconformity on the upper Oligocene Caimito Formation (Text-fig. 7). Westwards, the Gatun Formation can be traced as far as Gobea.

*Lithology.*—The lower five m of the lower Gatun Formation (Text-fig. 4) consists of volcanic conglomerate, with 1–5-cm clasts and a tuffaceous, arkosic matrix, cross-bedded, laminated, tuffaceous siltstone, and alternating laminated sandstone and siltstone, mostly deeply weathered. The overlying 40 m (Section 1) consists of massive, grey-green, clayey siltstone, with minor claystone and fine sandstone units. Zones of densely packed large concretions, pervasive bioturbation, and extensive thalassinoid burrow systems, as well as simple vertical and lateral hash-filled burrows, are typical of this part of the section. Shell hash of varying grain size and density is almost ubiquitous, as are units packed with diverse, whole mollusks.

The middle Gatun Formation (Text-fig. 4) is described in Section 2 and covers the composite section from Gatun to Margarita. The middle Gatun Formation is about 350 m thick and consists of alternating siltstone and sandstone with occasional 4–5-m units of interbedded sandstone and conglomerate. Concretion zones like those of the lower Gatun Formation are largely absent. Shell hash and diverse molluscan assemblages are somewhat less abundant than in the lower Gatun Formation, but pervasive bioturbation is still very extensive. Bentonitic horizons and a higher wood fragment content are also typical of the middle Gatun Formation.

The upper Gatun Formation (Text-fig. 4) is exposed around Mount Hope (upper part of Section 2) and more extensively on the western side of the canal, along and adjacent to the road to Piña (Section 4), and is about 40 m thick. The lithology is more consistently volcaniclastic sandstone or fine conglomerate, with minor mudstone and siltstone. Thin bentonite horizons and shell hash are common but diverse, whole mollusks are relatively rare. A distinctive horizon is exposed below the overflow dam on the Chagres River west of Gatun Locks (Map 1) and has conglomeratic, tuffaceous sandstone beds with extensive thalassinoid burrows, wood, and scattered coral colonies up to 50 cm in diameter. Armored mudballs, 6–10 cm in diameter, are also abundant at one horizon that has numerous pockets filled with conglomerate.

### The Chagres Formation

*Origin of the name.*—The Chagres Formation (Text-fig. 4) was named by MacDonald (1915) after the Chagres River.

*Location of stratotype.*—The stratotype is diagrammed in Section 3. It is exposed between Toro Point and Naranjitos Point (Map 1). A distinctive lateral facies of the Chagres Formation is exposed at Boca del Rio Indio (Map 1) on the north coast of Panama, approximately 40 km west of Colon. The Rio Indio facies is diagrammed in Section 5.

*Reference sections.*—Sections 3, 4, and 5 include the Chagres Formation, which has been recently revised by Collins *et al.* (1996). The formation also crops out along the coast as prominent cliffs between Toro Point, at Colon, and the mouth of the Chagres River (Map 1).

*Stratal relations.*—The Chagres Formation sits disconformably on the Gatun Formation; a marked change in lithology and a temporal hiatus characterizes the disconformity.

*Lithology.*—The Chagres Formation consists of indurated, conglomeratic, coarse-grained, volcanic sandstone with quartz, feldspar, and lithic grains. It is pervasively bioturbated and is relatively poor in macrofossils. Toward the west, in the region of the Indio River and Gobea (Map 1), the average grain size of the Chagres Formation markedly decreases and the macrofossil content increases.

#### *The Toro Member*

The base of the Chagres Formation at the stratotype, is distinguished by a distinctive echinoid-mollusk-barnacle coquina, about 60 m thick, which Woodring (1957) separated as the Toro Member (Text-figs. 4, 7). It is well exposed in the cliffs west of Toro Point, the headland on the northwest side of Colon Harbor (Map 1). The Toro Member has a middle portion characterized by about 10 m of steeply cross-bedded, prograding foreset beds, 2–50 cm thick, consisting of alternating coquina and shelly, coarse, volcaniclastic sandstone.

The Toro Member wedges out about 15 km to the southwest of Toro Point. Its restricted distribution at the northern end of the Panama Canal Basin, with high energy cross bedded coquina and very coarse volcaniclastics associated with bathyal Pacific benthic foraminifera, led Collins *et al.* (1996) to suggest deposition from a transisthmian strait in which strong currents flushed Pacific sediments and benthos into deep Caribbean waters.

## THE BOCAS DEL TORO BASIN

An extensive series of exposures of upper Neogene sediments can be observed in the coastal region of Bocas del Toro, Panama where they form an extensive archipelago (Text-fig. 2). Mapping has revealed a Miocene basement of widely distributed basalt lava, flow breccia, and coarse, pyroclastic and volcaniclastic sediments. The Bocas del Toro Group lies nonconformably on the underlying volcanics. The stratigraphic relations are shown in Text-figs. 5, 8a,b). The contact is well exposed in the Plantain Cays and on the coast south and west of Tobabe Point (Map 5, and inset B), where the volcanics form prominent bluffs of columnar basalt. Extinction, cooling, and subsidence of the volcanic arc locally in the region of the Bocas del Toro archipelago engendered a marine transgression represented by the Bocas del Toro Group.

The basal member of the Bocas del Toro Group is the Tobabe Sandstone, named herein. Messinian (7.2–5.3 Ma) in age, it represents a basal, transgressive, near-shore marine facies that gradually gives way to the upper bathyal facies (Collins, 1993) of the overlying Nancy Point Formation (Text-figs. 5, 8b). Continued regional elevation of the isthmus initiated, about 5 Ma, a shallowing upward sequence represented by the Shark Hole Point, Cayo Agua, and Escudo de Veraguas formations. This culminated in extensive, shallow marine, mixed volcaniclastic and coral reef deposits, about two Ma, many of which are exposed in unnamed units on Bastimentos and Colon islands (Text-fig. 8a). Also included is the early Pleistocene Swan Cay Formation (Text-fig. 5), a deep fore-reef deposit (Collins, Appendix 1, in Jackson *et al.,* this volume) exposed only on Swan Cay, a small island immediately north of Colon Island (Map 9). The new Tobabe sandstone and Swan Cay formations are here added to the Nancy Point, Shark Hole Point, Cayo Agua, and Escudo de Veraguas formations (Coates *et al.,* 1992) to form the expanded Bocas del Toro Group.

### The Tobabe Formation

*Origin of the name.*—The formation is named after the Guaymi village of Tobabe, located on the north coast of the Valiente Peninsula near the Plantain Cays (Maps).

*Location of stratotype.*—The stratotype is on Small Plantain Cay; a small, unnamed island immediately to the west; and for about one km along the coast, between Tobabe Point and the village of Tobabe (Inset B of Map 5).

*Reference sections.*—Section 14 describes a lateral variation of the Tobabe Formation exposed on the Toro Cays, south of the entrance of Bluefields Bay, at the western end of the Valiente Peninsula (Inset B of Map 5).

*Stratal relations.*—The Tobabe Formation sits nonconformably upon the Miocene basement of basalt lavas, flow breccias, and volcaniclastic sediments. It passes conformably up into the overlying Nancy Point Formation (Text-fig. 8b).

*Lithology.*—The Tobabe sandstone is the oldest unit of the Bocas del Toro Group. At the stratotype (Section 12) the basal unit of the Tobabe sandstone is a pebble and cobble conglomerate, about 15 m thick, with a variety of sedimentary and volcanic subangular clasts. It is unfossiliferous in its basal portion, but contains scattered, thick-shelled mollusks and occasional echinoids in the upper part, which grades insensibly into the overlying quartz sandstone that forms the rest of the formation. The sandstone is relatively clean, indurated, massive and pervasively bioturbated, although thin but persistent horizons of pebble conglomerate occur and larger volcanic cobbles are scattered throughout. Well-preserved burrows are present with particularly good examples of *Ophiomorpha* and thalassinoid burrows. The unit is distinguished by very abundant, large, thin-shelled *Amusium,* numerous large sand dollars and spatangoid echinoids. Other mollusks are present as low-diversity, poorly preserved molds. Occasional specimens of wood bored by *Teredo,* and worms, including serpulids and vermetids, are also present.

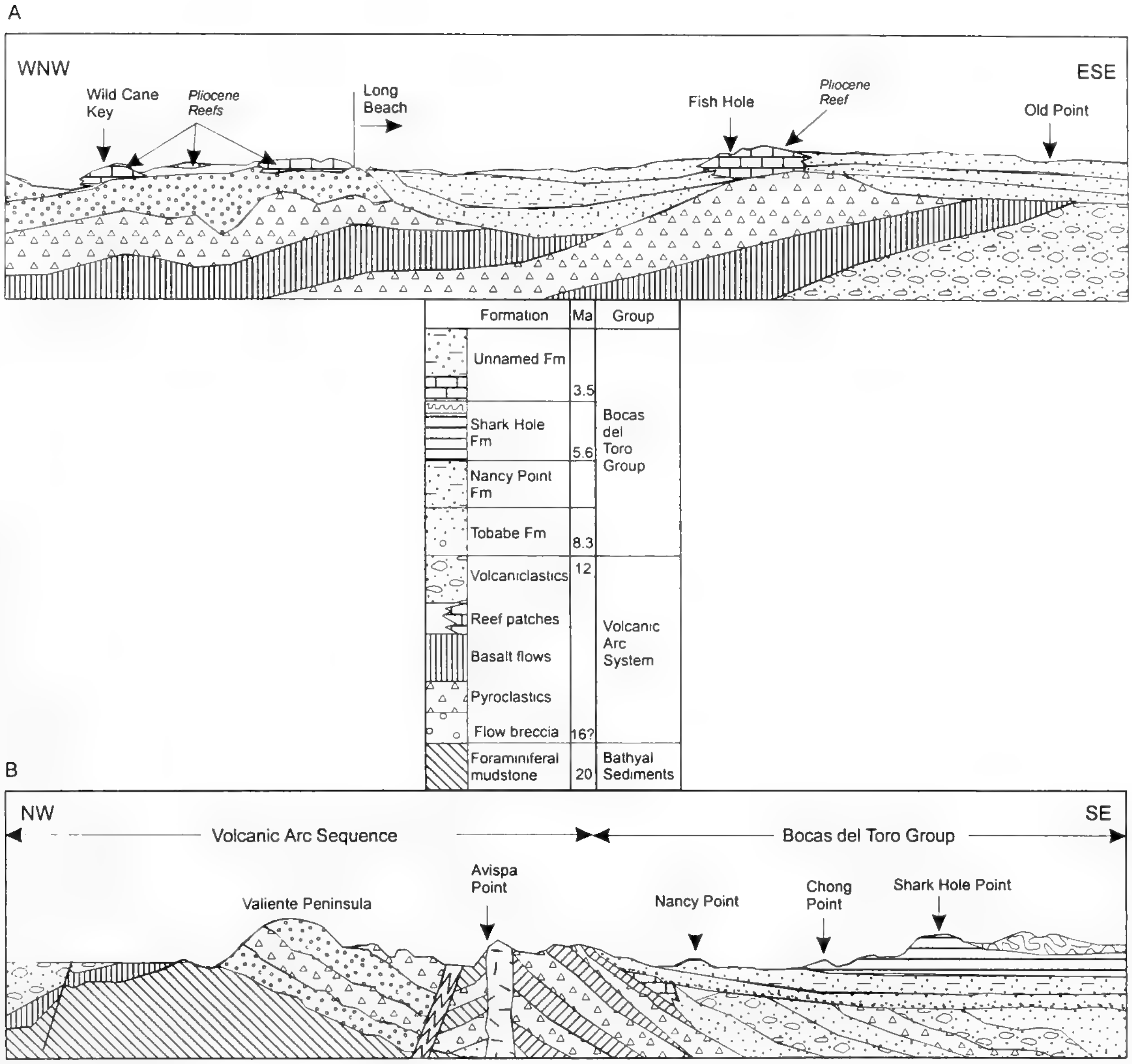
The Tobabe Formation cropping out on the Toro Cays (Section 14), is about 30 m thick. The lower 20 m consists of extensively burrowed, coarse, quartz and lithic volcanic sandstone with abundant and elaborate thalassinoid burrow systems, alternating with beds of 1-m-thick basalt and sandstone conglomerate, and occasional thin siltstone and muddy sandstone units containing scattered turritellids and other mollusks. The upper 10 m of the Tobabe Formation on the Toro Cays is composed of massive, shelly, volcaniclastic, relatively clean bioclastic sandstone, with strongly cross-cutting, laminated channels. Spectacularly large, shell-filled burrows about 10–15 cm in diameter are very characteristic, as is pervasive burrow mottling, and in other horizons, vertical 1–3 cm burrow tubes. Thick-shelled mollusks, including pectens, erect bryozoans and spatangoid echinoids, are common.

### The Nancy Point Formation

*Origin of the name.*—The Nancy Point Formation (Text-fig. 5; Sections 12,15) was named by Coates *et al.* (1992), for the promontory called Nancy Point which lies 2.5 km south of the village of Tobabe (Map 5).

*Location of stratotype.*—The stratotype of the Nancy Point Formation lies along the northern coast of the Valiente Peninsula, starting at Nancy Point and running south to near Chong Point (Map 5, and insets D, E, F).

*Reference sections.*—There are no exposures between the stratotypes of the Nancy Point and the Tobabe Sandstone along the north coast of the Valiente



Text-figure 8.—a. Schematic geologic cross section along the north coast of Bastimentos Island showing younger unnamed formations of the Bocas del Toro Group unconformably overlying the volcanic arc deposits. b. Schematic geologic cross section from the western tip of the Valiente Peninsula to Shark Hole Point, showing the volcanic arc deposits unconformably overlain by the older units of the Bocas del Toro Group.

Peninsula. Assuming a constant dip (the type Tobabe and Nancy Point Formations have the same strike and dip), 400 m of section are not exposed. Much of this missing interval is exposed on the southern coast of the Valiente Peninsula between Warrie Point and the southern headland of the small peninsula of Toro Point (Map 5), and is diagrammed in Section 15. Lithologically it appears to be more typical of the Nancy Point Formation.

*Stratal relations.*—The Nancy Point Formation is conformable with the Tobabe Formation below and the Shark Hole Point Formation above (Text-fig. 8b).

*Lithology.*—The Nancy Point Formation consists of massive, pervasively bioturbated, shelly, muddy and silty sandstone, muddy siltstone, with scattered mollusks and occasional leaves and plant fragments, and occasional coarse volcaniclastic and bioclastic sandstone beds. There are several low-diversity shell beds (Section 15) near the base and several diverse moderately abundant molluscan assemblages throughout the section. The base of Section 15, on the south coast of the Valiente Peninsula has a faulted contact with the underlying volcanics so that no typical Tobabe Sandstone crops out.

The transition from Tobabe Formation to Nancy Point Formation deposits is best seen on Toro Cay

(Map 5, inset A), where dark blue-gray, silty sandstone, typical of the Nancy Point Formation, contains occasional, clearly defined 50-cm-thick thalassinoid burrow systems and extremely abundant and diverse mollusks. It overlies coarse, channeled Tobabe sandstone with only a 10-m gap. The transition from the Tobabe sandstone to the Nancy Point Formation thus appears to be conformable and to involve relatively rapid deepening from nearshore to upper slope facies.

### The Shark Hole Point Formation

*Origin of the name.*—The Shark Hole Point Formation was named by Coates *et al.* (1992) for the promontory of the same name that lies 3 km east of Chong Point (Map 5).

*Location of stratotype.*—The stratotype lies along the coast between Chong Point and Bruno Bluff (Map 5, and inset F).

*Reference sections.*—Section 15, along the south coast of the Valiente Peninsula contains the Shark Hole Point Formation as is indicated on Text-figure 5.

*Stratal relations.*—The Shark Hole Point Formation conformably overlies the Nancy Point Formation (Text-fig. 8b) and is overlain by an unnamed conglomeratic, cross bedded, coarser grained sequence of volcaniclastics containing large pieces of wood and plant fragments. This unnamed unit is exposed only along the southern coast of the Valiente Peninsula, east of Secretario (Map 5).

*Lithology.*—The formation is about 200 m thick and consists of micaceous, clayey siltstone that is pervasively bioturbated and rich in large scaphopods. The uppermost part of the formation also contains abundant, thin, shelly beds and intraformational slumps with pillow folds and rip-up clasts.

### The Escudo de Veraguas Formation

The stratigraphic order of the formations described above has been determined by physical superposition. The three remaining formations of the Bocas del Toro Group are known only on islands and their position relative to the other units has been determined by biostratigraphic evidence discussed in Appendix 1, (this chapter).

*Origin of the name.*—The Escudo de Veraguas Formation (Text-fig. 5) was named by Coates *et al.* (1992) for the island of the same name that lies about 27 km east of Nancy Point (Map 4).

*Location of the stratotype.*—The original stratotype, defined by Coates *et al.* (1992), is located along the north coast (Map 4, inset A and B), from Long Bay Point one km eastward (lower part of the formation), and for two km south of Long Bay Point on the west coast (upper part of the formation). We have since carried out more detailed field work that indicates that the coastal section immediately east of Long Bay Point is essentially along strike and thus probably exposes the same sequence of beds several times. A continuous section for the lower part of the formation is best obtained along the coast on the east side of the V-shaped embayment situated in the center of the north coast about two km east of Long Bay Point (Map 4C). This locality is now defined as the stratotype for the lower part of the Escudo de Veraguas Formation. The stratotype for the upper part of the formation remains that originally defined by Coates *et al.* (1992) along the west coast for one km south of Long Bay Point. Between these upper and lower stratotypes, both of which have clearly documented physical superposition of strata, there is a small but unknown amount of section missing. The exposures along the north coast of Escudo de Veraguas, immediately east of Long Bay Point, and west of the V-shaped embayment in the center of the north coast, which were part of the original stratotype defined by Coates *et al.* (1992), are estimated to fall in this gap. However, because the coast is irregular and only approximately parallel to strike, the stratigraphic order of samples from these exposures can not be determined. Collectively these samples were dated as 1.8–1.9 Ma and because they underlie the upper stratotype, they constrain it to be younger than 1.8–1.9 Ma.

*Stratal relations.*—The upper and lower contacts of the Formation are not exposed.

*Lithology.*—The lowest 10 m of the formation at the stratotype is moderately indurated, fine, silty sandstone and clayey siltstone, pervasively bioturbated and containing frequent, cemented, irregular burrow-concretions and horizons with dense thalassinoid burrow systems. The overlying 30 m of clayey siltstone, silty claystone and silty, fine sandstone is also pervasively bioturbated, with frequent concretions, thalassinoid burrows and scattered mollusks with a distinctive basal 2 m thick marker bed rich in corals and mollusks.

Following 70 m of no exposure, the section continues with 13 m of clayey bioclastic siltstone, with some angular basalt grains, scattered mollusks and cupuladrian bryozoans. The section is massive and pervasively bioturbated with scattered fine shell hash. About 5 m from the top, a second marker horizon is defined by a densely packed coral biostrome that is also rich in echinoids and mollusks. The lower part of the Escudo de Veraguas Formation 2.6–3.5 Ma.

The upper part of the Escudo de Veraguas Formation (Section 10) consists of about 8 m of blue-gray, clayey siltstone and silty claystone, sparsely shelly and intensely burrow-mottled. Thalassinoid-type burrows are common, as are echinoids; the latter are very fragile and almost impossible to collect. Two distinctive marker beds within this section consist of slightly more indurated burrow zones, suggesting minor disconformities or slower depositional rates.

### The Cayo Agua Formation

*Origin of the name.*—The Cayo Agua Formation (Text-fig. 5) was named by Coates *et al.* (1992) for the island of the same name in the Bocas del Toro archipelago, that lies about six km to the west of Toro Point, Valiente Peninsula (Map 6, and insets of Map 6).

*Location of stratotype.*—More detailed section measuring on Cayo Agua has revealed that the stratotype is slightly more complex structurally than indicated by Coates *et al.* (1992). The stratotype for the formation (Section 19) is now calculated to be slightly thinner because a small block immediately to the south of Nispero point is rotated to dip to the northeast and repeats a portion of the section (Section 20). The newly defined stratotype (Section 19 runs from just south of North Point along the east coast southward to Nispero Point, and then from the northernmost to the southernmost exposures on the coast surrounding Tiburon Point.

*Reference sections.*—Additional reference sections are Section 16, immediately west of North Point; Section 18, north of Red Rock Point; and Section 17, on the south coast immediately west of Red Rock Point The stratigraphic relations of these sections are shown in Text-figure 5.

*Stratal relations.*—The Cayo Agua Formation is equivalent in age to the upper part of the Shark Hole Point and the lower part of the Escudo de Veraguas formations and represents a shallower water facies. No contacts are known.

*Lithology.*—The Cayo Agua Formation is distinguished lithogically as a pervasively bioturbated gray blue, muddy, silty lithic sandstone with common horizons of abundant thick shelled mollusks and ahermatypic corals. Occasional horizons of pebble conglomerate and very coarse-grained volcaniclastic sandstone are common in the middle of the formation. Compared to the Shark Hole and Escudo de Veraguas formations, the Cayo Agua Formaton is consistently coarser-grained, with common basalt grains and granules, phosphatic pebbles, and wood fragments. A distinctive marker bed of packed ahermatypic corals occurs near the top of the formation and is well exposed at Tiburon Point (Map 6) and the unnamed point to the south. In addition the mollusks and corals in the Cayo Agua Formation are larger and more heavily calcified than those of the Shark Hole and Escudo de Veraguas formations. Evidence from benthic foraminifera (Collins, 1993) confirms the inference from grain size and fauna that the Cayo Agua Formation represents a more shallow-water facies than either the Shark Hole or Escudo de Veraguas formations.

### The Swan Cay Formation

*Origin of the name.*—The Swan Cay Formation is named for the small island of the same name that lies 1.7 km off the north coast of Colon Island (Map 9).

*The location of the stratotype.*—The stratotype (Text-fig. 5; Section 25) is the section that runs from north (youngest) to south (oldest) across Swan Cay.

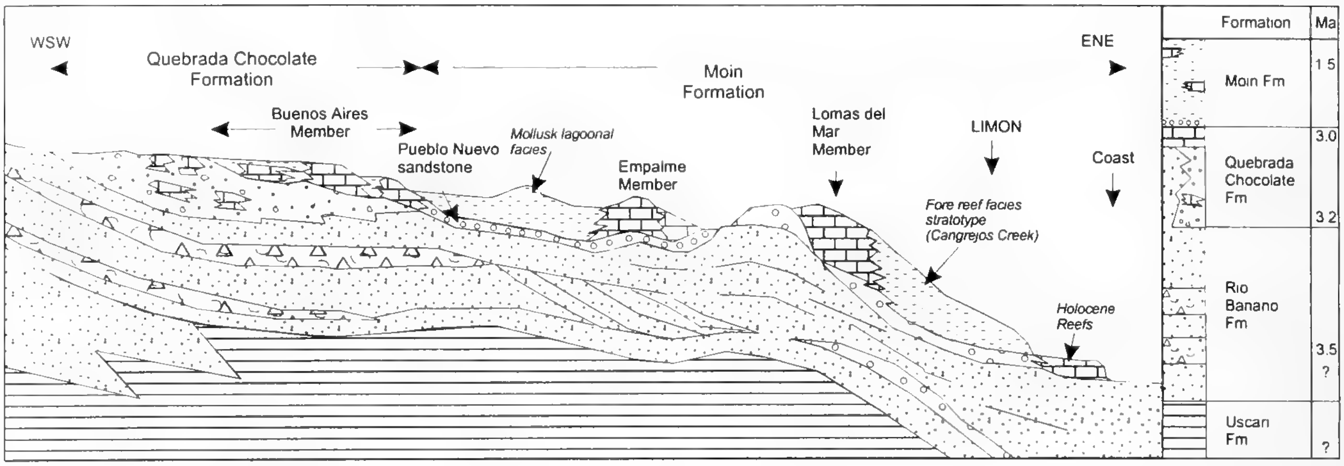
*Reference sections.*—No other sections of the Swan Cay Formation have been observed.

*Stratal relations.*—No contacts are observed but the stratigraphic relationship of the Pleistocene Swan Cay Formation, within the Bocas del Toro Group, based on biostratigraphic data, is shown in Text-figure 5.

*Lithology.*—The formation has three components. The lower 15 m is exposed on the southerly low hill of the island and consists of silty sandstone and shelly calcarenitic siltstone, with coral rubble and red algal fragments and balls. The middle four m consists of calcarenitic clayey siltstone, with dense, fine shell-hash horizons, and abundant large coral colonies in the lower part. The upper 60 m of the formation consists of massively thick-bedded, pale tan-white calcarenite. The upper 30 m are vuggy, sparry, and clean and include a 4-m-thick coral bed with large *Montastraea* colonies, other corals and mollusks. The lower 30 m consist of more silty calcarenite with common red algae and large foraminifera, shell hash, and micromollusks. Cave deposits, about five m above the base of the calcarenite, consist of silty, shelly, volcaniclastic sandstone, mixed with abundant volcanic cobbles and boulders, and calcareous reef rubble containing an abundant and diverse molluscan assemblage.

## THE LIMON BASIN

The southern part of the Limon Basin is located on Text-figure 2. The tectonic sedimentary history of the southern Limon Basin was recently reviewed by Bottazzi *et al.* (1994). They analyzed Campanian to Pleistocene sequences in detail, utilizing surface and subsurface data that were generated by petroleum exploration since 1957. They list four upper Neogene units; the older Uscari and Rio Banano formations and the younger Suretka (terrestrial) and Limon (marine) formations. In a previous publication, Coates *et al.* (1992) grouped these sediments (excluding the Suretka Formation) in the Limon Group. However, the sediments of the Limon Formation (for which Bottazzi *et al.* (1994) give no type locality) were previously included in the Moin Formation, recognized originally by Gabb



Text-figure 9.—Schematic geologic cross section across the southern Limon Basin from Chocolate Creek to the Port of Limon, slightly modified from McNeill *et al.* (in press).

(1881) and Taylor (1975), and given formation status by Cassell (1986), Cassell and Sen Gupta (1989a), Coates *et al.* (1992) and Collins *et al.* (1995). The name Moin thus has priority over Limon for this unit.

A recent detailed analysis of the upper Neogene sediments of the region immediately west of Limon, that combined litho- and biostratigraphy with paleomagnetic analysis (McNeill *et al.,* in press), confirmed the Moin Formation as the youngest unit of the Limon Group. It also named a new unit, the Quebrada Chocolate Formation, that conformably overlies the Rio Banano Formation and underlies the Moin Formation (Text-fig. 6). The four formations of the Limon Group represent a genetically coherent, shallowing upward, marine, sedimentary sequence that reflects the rise of the Central American isthmus. Elsewhere in the southern Limon Basin, the Quebrada Chocolate and Moin Formations are laterally replaced by the Suretka Formation (Bottazzi *et al.,* 1994), which consists of terrestrial (alluvial) volcanic conglomerate and breccia.

Some of the reef deposits now included in both the Quebrada Chocolate and Moin formations were erroneously identified by Coates *et al.* (1992, pp. 822, Fig. 7) as overlying, younger Pleistocene Reef Limestone. In part this was because these reef deposits commonly contain *Acropora palmata,* which was widely accepted to be restricted to the Pleistocene. Subsequent facies analysis by McNeill *et al.* (in press), and identification of the coral fauna by Budd *et al.* (this volume), have established that this Reef Limestone consists of several reef members interbedded with the Pliocene to lowermost Pleistocene siliciclastic and bioclastic sediments of the Quebrada Chocolate and Moin Formations. The stratigraphic relations of the formations of the Limon Group are shown in Text-figures 6, 9.

In the southern Limon Basin, during the Early and Middle Miocene, sedimentation was dominated by bathyal, fine-grained, siliciclastic deposits typified by the oldest unit of the Limon Group, the Uscari Formation (Cassell and Sen Gupta, 1989b; Collins *et al.,* 1995). While these sediments contain a rich microfauna, to date, they have not yielded abundant macrofossils. Throughout the southern Limon Basin, the Uscari lithofacies is replaced diachronously by coarser, more variable, shallow-water sediments, interpreted as a nearshore marine and deltaic sequence, whose provenance was the rising Talamanca Range to the southwest. This near-shore marine and deltaic facies, represented by the Rio Banano Formation, replaced the bathyal facies, represented by the Uscari Formation, during the latest Miocene. By the Pliocene, these facies were present throughout most of the southern Limon Basin (Bottazzi *et al.,* 1994). The Rio Banano Formation is highly variable in lithology, consisting of interfingering marine delta-front and delta-plain deposits, and locally containing well-preserved, abundant, diverse, shallow-marine faunal assemblages.

By the late Pliocene and Pleistocene, much of the southern Limon Basin had become emergent so that the marine deposits are unconformably overlain by coarse alluvial conglomerate and breccia, comprising the Suretka Formation. However, in the vicinity of Limon, marine deposition continued until the early Pleistocene, forming shallow-water, brackish and normal-marine claystone, sandstone, and reef deposits that represent lagoonal, mangrove, and seagrass habitats, interfingering with a variety of tabular and patch reefs (Text-fig. 9). These deposits comprise in part the Quebrada Chocolate and Moin formations. The Quebrada Chocolate Formation is, in part, coeval with the upper portion of the Rio Banano Formation in its type area near Bomba on the Banano River (Text-fig. 6).

The development of active folds and faults associated with the active North Panama Deformed Belt, in association with the insertion of the Cocos Ridge (Collins *et al.*, 1995), has meant continued rapid uplift of the Limon Group deposits. Today, the youngest unit, the Pleistocene Moin Formation, is now 40 meters or more above sea level. Modern reef deposits around Limon rose a maximum of 1.7 m in the earthquake of 1991 to form emergent coastal terraces, indicating that uplift continues.

The presence of *A. palmata* (McNeill *et al.*, 1997) in the upper Pliocene Buenos Aires Member (about 35 Ma) of the Quebrada Chocolate Formation is now the oldest known record of the species.

### The Uscari Formation

*Origin of the name.*—The Uscari Formation (Text-fig. 6) was first named informally by Berry (1921) and later formalized by Olsson (1922) for deposits along the Uscari Creek, a tributary of the Amoura River that runs into the Sixaola River.

*Location of the stratotype.*—The original stratotype was not precisely located along the Uscari River and is probably not now exposed.

*Reference sections.*—The lack of good exposures at the original type locality led Cassell and Sen Gupta (1989a) to designate a new reference section along the Terciopelo Creek, about 62 km due west of Limon. The Uscari Formation also crops out widely in the southern Limon Basin, where it has been described by several authors (Olsson, 1922; Redfield, 1923; Palmer, 1925).

*Stratal relations.*—The Uscari Formation passes abruptly, although conformably for the most part, into the coarser grained strata of the overlying Rio Banano Formation. However, this transition is strongly diachronous across the southern Limon Basin.

*Lithology.*—The early authors, noted above, described the Uscari Formation as a friable, gray claystone, rich in montmorillonite, with minor limestone and calcareous sandstone, and a thickness between 600 and 1500 m. Later, Olsson (1942) proposed a two-fold division into a lower black shale, typically occurring around the type area, and the "upper grey shales", separated by a "*Dentalium* Zone". He noted that the upper unit contains sandstone and conglomerate, and is typically developed between Puerto Viejo on the coast and the Panamanian border to the south.

The reference section described by Cassell and Sen Gupta (1989a) consists of a basal biocalcarenite, 12 m thick, formed of larger foraminifera and red algal rhodoliths interbedded with sandstone rich in pyroxene and foraminifera, that is overlain by 550 m of well-bedded, soft, dark shale, rich in planktic foraminifera. Foraminifera of the Uscari Formation were described by Goudkoff and Porter (1942), Cassell (1986) and Cassell and Sen Gupta (1989a, b), and an extensive facies analysis was given by Bottazzi *et al.* (1994). In this study, in the extreme south of the Limon Basin, claystone sections were measured near Carbon Dos, (Map 10; Section 28), and at the Sandbox River, near Catarata (Map 10; Section 27), both representing bathyal conditions (Collins *et al.*, 1995). In the Sandbox River section, the claystone is overlain disconformably by a basal conglomerate of the deltaic Rio Banano Formation. In the area of the Banano River, southwest of Limon, Taylor (1975) described a conformable transition of increasing grain size between the Uscari Formation and the overlying Rio Banano Formation.

### The Rio Banano Formation

*Origin of the name.*—The name Rio Banano Formation is taken from the Banano River which flows into the Caribbean about nine km south of Limon.

*Location of the stratotype.*—The formation was named by Taylor (1975) but the stratotype (Text-fig. 6) was designated by Cassell (1986) as the bluffs on the Banano River, 500 m southwest of the railroad bridge at Bomba.

*Reference sections.*—The stratotype was measured by Coates *et al.* (1992), who extended the section along the Banano River from just west of Quitaria to the railroad bridge at Bomba (Inset C of Map 11, Section 29). In addition to the stratotype, sections of the Rio Banano Formation (Map 11) have been measured on the Bananito (Section 31), Peje (Section 30) and Vizcaya (Section 39) rivers and at Santa Rita (Section 32).

*Stratal relations.*—The Rio Banano Formation sits diachronously with abrupt lithological transition on the Uscari Formation, mostly conformably and sometimes disconformably. The Rio Banano Formation passes conformably into the Quebrada Chocolate Formation (Text-fig. 9) in the area immediately west of Limon but throughout most of the southern Limon Basin it is unconformably overlain by the breccia and coarse grained volcaniclastics of the Suretka Formation.

*Lithology.*—Some of the rocks designated by Taylor as the Rio Banano Formation were first recognized as a lithological unit by Howe (1907) and subsequently correlated with the Gatun Formation of Panama by Olsson (1922). Taylor's (1975) definition of the Rio Banano Formation included not only the dominant sandstone lithofacies that crops out at the type locality but also a conglomerate, reef and claystone facies. Subsequently, Cassell and Sen Gupta (1989a) and Coates *et al.* (1992) restricted the formation to the sandstone unit and separated the reef and claystone lithologies as the overlying Quebrada Chocolate and Moin formations and their respective reef members.

The sections at Quitaria (Section 29) and Bomba (Section 29) show two relatively thin, richly fossiliferous marine units within a thick deltaic section of burrow-mottled, coarse, tuffaceous, concretionary sandstone that frequently contains basalt pebbles, leaves, seeds, and wood fragments. The lower marine section is exposed along the road and adjacent river bank, about 200 m east of the banana loading station at Quitaria (inset C, Map 11). About 15 m of burrow-mottled, shelly, clayey siltstone and silty, tuffaceous sandstone contain frequent shelly stringers and lenses that contain an abundant and diverse marine mollusk and bryozoan assemblage. Thalassinoid burrow systems are common, often packed with shell hash, as are slabby and irregular concretion zones. The upper marine section is well exposed on both the north and south banks of the Banano River approximately 500–700 m southwest of the railway bridge at Bomba (Inset C, Map 11). The lower part of the section crops out on the north bank and is about 17 m thick. It consists mostly of blue-gray, burrow-mottled, clayey siltstone with scattered, fine, volcanic pebbles. The unit is rich in diverse mollusks, including scaphopods, and in bryozoans. The remaining part of the marine section is exposed on the south bank of the Banano River immediately to the east of the lower unit. The section contains 10 m of massive, sporadically fossiliferous and finer grained, tuffaceous siltstone at the base. Pervasive bioturbation is common, with slabby and irregularly rounded concretions and occasional richly shelly zones. This is overlain by 6 m of dominantly blue-gray, tuffaceous, silty sandstone with scattered volcanic pebbles and abundant burrow systems, packed with shell hash and volcanic pebbles. Some horizons are rich in spatangoid echinoids and all are very rich in diverse and well-preserved mollusks.

The marine units described at the type locality appear to persist along strike and were measured in the Vizcaya and Bananito rivers (Map 11). The section in the Vizcaya River extends upwards into a distinctive shoreface facies. It is dominated by coarse, laminated sandstone, with low angled, prograding foreset beds, discrete, complex, thalassinoid burrow systems as well as large, circular, vertical burrows. The molluscan assemblages of these units are less diverse than in the stratotype, and are often dominated by *Docinia*; cupuladrian bryozoans are also common. Fine pebble- to granule-sized volcanic clasts are common and 1-cm diameter phosphatic pebbles are also present.

The section in the Peje River (Map 11) is the highest in the Rio Banano Formation and is correspondingly more proximally deltaic (German Gonzalez, oral commun., 1992). The section is relatively unfossiliferous, dominated by volcanic conglomerate and sandstone. Rip-up clasts, dispersed, low-diversity mollusks, wood fragments, and large seeds are common.

The Rio Banano Formation crops out extensively in other parts of the southern Limon Basin (Bottazzi *et al.*, 1994), where sequences have been interpreted as representing estuarine-bay, fan-delta, delta-plain, delta-front, and shoreface facies.

## The Quebrada Chocolate Formation

*Origin of the name.*—The formation is named for the Chocolate Creek that flows north into the Caribbean, crossing Route 32 at Buenos Aires, about six km west of Limon.

*Location of the stratotype.*—McNeill *et al.* (in press) have recently revised the stratigraphy and paleoenvironmental interpretation of the Limon Group in the region of Limon. They established the stratotype of their new Quebrada Chocolate Formation (Text-figs. 6, 9) along Chocolate Creek for about two km south of Route 32 and along Route 32 from Buenos Aires to 1.2 km east of the junction of Route 32 and Route 240 (Old Moin road).

*Reference sections.*—There are no other measured sections in the Quebrada Chocolate Formation, which only crops out in a restricted area west of Limon (McNeill *et al.*, Text-fig. 2, in press)

*Stratal relations.*—The Quebrada Chocolate Formation conformably overlies the Rio Banano Formation and is conformably overlain by the Moin Formation.

*Lithology.*—The Quebrada Chocolate Formation (Section 33) consists of coarse, volcaniclastic, clayey siltstone and sandstone, conglomerate, calcarenite, and reef-rubble limestone. In the lower part there are thin, low-diversity, recrystallized reef lenses with corals in growth position. The base of the Quebrada Chocolate Formation lies at the waterfall on Chocolate Creek, 1.5 km south of Route 32, where the first reef member is composed dominantly of *Porites* in a clayey siltstone matrix. This unit is overlain by shelly, volcaniclastic sandstone with extensive thalassinoid burrow systems, coarsely laminated, cross-bedded sandstone, fine conglomerate, reef rubble, and calcarenite. Corals from these units are abundant and diverse (Budd *et al.*, this volume) but associated flank rubble and sandstone also contain a large, thick-shelled *Spondylus* and many small bivalves and oysters.

### *The Buenos Aires Member*

The top of the Quebrada Chocolate Formation consists of a series of extensive tabular reefs that is separated as the Buenos Aires Reef Member (Text-figs. 6, 9). It is named for the village of Buenos Aires, on Route 32 six km west of Limon, where it forms a low but distinct topographic feature. The stratotype is located from the intersection with Chocolate Creek east along Route 32 for 1.2 km. The Buenos Aires Reef Member (Section 33) is about 140 m thick and consists of a series of coral thickets with a silty claystone matrix, dominated by *Porites, Acropora, Stylophora, Caulastrea,* and agariciids. Interbedded with the reefs are coral- and mollusk-rich carbonate sandstone and siliciclastics. The top of the Buenos Aires Reef Member has an interfingering contact with the grey-blue claystone, siltstone, and channeled sandstone of the base of the Moin Formation.

### The Moin Formation

*Origin of the name.*—The formation is named for the small port of Moin, at the mouth of the Moin River, about six km west of Limon.

*Location of the stratotype.*—The name Moin was first used by Gabb (1881) for the dark claystone and muddy sandstone along the coast between Moin and Limon. He named these deposits the "Moin Member" without specifying a stratotype. Taylor (1975) included the Moin Member in his broadly defined Rio Banano Formation. He specified the stratotype as the small, unnamed creek that flows northwestward from near the Barracuda road, about two km west of Limon, through the Cangrejos housing complex (Inset B, Map 11), which lies south of the main coastal road at Playa Bonita.

*Reference sections.*—Sections 35, 36, and 38, in the Lomas del Mar suburb of western Limon. These include the Empalme and Lomas del Mar reef members described below.

*Stratal relations.*—The Moin Formation sits conformably on the Quebrada Chocolate Formation and has no upper contact.

*Lithology.*—The Moin Member was established as a formation by Cassell (1986) and Cassell and Sen Gupta (1989a), and was expanded in concept by Coates *et al.* (1992) to include its biostromal reef members as well as other lithologies now separated as the Quebrada Chocolate Formation.

The Moin Formation (Text-figs. 6, 9) is here retained with Taylor's originally designated stratotype along the creek that runs through the Cangrejos subdivision (Section 37). It consists of blue-gray, silty claystone and blocky, muddy, shelly, volcaniclastic sandstone, with common basalt granules. Also present are scattered mollusks and callianassid burrows, and the lower part of the section contains laminated, pyritic, organic-rich claystone and erect, branching bryozoans. In general, siliciclastic sediments in the Moin Formation are finer grained than in the Quebrada Chocolate Formation.

The reef members of the formation cap the high ground that forms a plateau at about 40 m of elevation immediately to the northwest of Limon. To the west of the plateau, the lower Moin Formation is evident in sporadic exposures to the north of Route 32, until about four km west of Limon. Alternating thin units of shelly, blue-grey siltstone and claystone, extremely rich in diverse mollusks, bryozoans, crabs, and oyster beds, alternate with sandstone, often containing dense, callianassid burrow systems, thin, small, coral-rich patch reefs, and tight, dark claystone with mangrove root systems, logs, and wood fragments. McNeill *et al.* (in press) separated two major reef build-ups as members within the upper Moin Formation, as described below.

### *The Empalme Member*

Interbedded with the mollusk-rich claystone and siltstone of the lower Moin Formation is the first of the two major reef trends within the formation (Section 34). McNeill *et al.* (in press) named the Empalme Reef Member (Text-fig. 6) for the small settlement of Empalme Moin near the intersection of Route 240 and the Empalme Moin to Limon Road. This unit is usually deeply weathered and poorly exposed, but temporary, fresh exposures near Route 240 (Insets A, B, Map 11), Empalme Moin, and west of Pueblo Nuevo Cemetery, reveal calcarenite, carbonate sandstone, and coral-rich sandstone, dominated by the hermatypic corals *Porites, Montastraea, Stephanocoenia, Caulastrea, Diploria,* and agariciids.

### *The Lomas del Mar Member*

The youngest and most fossiliferous of the reef units, the Lomas del Mar Member (Text-fig. 6), is about 30 m thick and caps the plateau immediately to the west and northwest of Limon from 45–60 m in elevation (Text-fig. 9). Extensive fresh sections in the Lomas del Mar Reef Member were exposed at two sites that were bulldozed down to bedrock for housing projects. The eastern of these (Section 36) is now covered by houses; as of 1998, the western section (38) was exposed south of Barracuda Avenue 300–800 m. west of the intersection with King Fish road. There are also scattered exposures underlying and lapping against the Lomas del Mar Member of a deeply weathered, unfossiliferous, coarse sandstone, named by Taylor (1975) the Pueblo Nuevo Sandstone.

The Lomas del Mar Member consists of three lithofacies (Sections 36–38):

1) Bioclastic, rubbly, reef limestone forming irreg-

ular lensing patches, each 20–50 m in diameter, and about 1–3 m in maximum thickness. The patches yield abundant large coral heads, particularly *Montastraea cavernosa* and *Dichocoenia,* and a diverse and abundant array of small colonies, including several species of *Montastraea, Agaricia, Mycetophyllia,* and *Dichocoenia,* as well as numerous, slender, branching colonies of *Madracis asperula* (Budd *et al.,* this volume)

2) Blue-grey, clayey siltstone and calcarenite that form flank beds immediately adjacent to the reef patches. Sediments are packed with small, diverse mollusks, including vermetids, small solitary and oculinid ahermatypic corals, bryozoans, especially cupuladrians, serpulids, and large echinoid spines. The reef facies laterally interfingers with these flank beds at the Cangrejos creek stratotype (Section 37).

3) Massive, blocky, grey-blue claystone between the reef patches with scattered mollusks and fine shell hash.

## CONCLUSIONS

The Neogene stratigraphy of three depositional basins along the Caribbean coast, from Limon, Costa Rica to the Panama Canal, is revised and several new formations created. Eleven maps plus detailed insets and 39 sections are presented in Appendices A and B, respectively, giving the location of all PPP samples studied for this volume and their stratigraphic position and relations.

The Middle and Upper Miocene Gatun and Chagres formations of the Panama Canal Basin form an apron of marine sediments flanking the isthmian volcanic arc. In the Bocas del Toro Basin, in western Panama, an Upper Miocene to Pleistocene sequence, the Bocas del Toro Group, forms an apron of inner to outer neritic marine sediments, comprising six formations, that overly a Middle Miocene basement of basalt and coarse volcaniclastics. The Miocene to Pleistocene marine deposits of the southern Limon Basin consist of a shallowing upward (bathyal to inner neritic) series of four Neogene formations that form the Limon Group.

### THE PANAMA CANAL BASIN

The Gatun Formation is described from four reference sections. The lower and middle part of the section is well exposed between Sabanita and Payardi (Sections 1, 2) and the upper part near Toro Point (Section 3) and Piña (Section 4). The Gatun Formation lies unconformably on the Cretaceous volcanics in the eastern part of the basin and on the Caimito Formation in the west. It consists of about 500 m of volcaniclastic bioturbated gray-green claystone, siltstone and sandstone, with large concretions and shell beds packed with mollusks in the lower part and coarser sandstone and fine conglomerate in the upper part.

The Chagres Formation lies disconformably on the Gatun Formation. Locally, near Colon, the Chagres is distiguished by a basal member, the Toro Point, which is an echinoid-barnacle-mollusk coquina, in part strongly cross-bedded with coarse sandy to pebbly volcaniclastics, deposited in bathyal water depths and containing dominantly Pacific benthic foraminifera.

Four small sections were measured along the North Coast of Panama (Sections 6, 7, 8, and 9) but are not currently assigned to any formation. In age and lithological affinity they most resemble the Gatun Formation.

### THE BOCAS DEL TORO BASIN

The Neogene sediments of the Bocas del Toro Basin are represented by the Bocas del Toro Group. The most continuous Neogene section lies along the north and south coasts of the Valiente Peninsula (Sections 12, 15). Here, the Bocas del Toro Group sits nonconformably on the underlying columnar basalt, basalt flow breccia, coarse volcaniclastics, and coral reef lenses of the Middle Miocene "basement". The section ranges from Upper Miocene (Messinian, 7.1–5.3 Ma) to upper Pliocene (3.5 Ma). Younger deposits are found on Escudo de Veraguas island (Sections 10, 11; 3.5–1.8 Ma) and Bastimentos, Colon, and Swan Cay islands (Sections 21–26; ~2.0–1.5 Ma) and a more shallow water facies of the lower Pliocene is found on Cayo Agua island (Sections 16–20; 5.0–3.5 Ma).

The basal unit of the Bocas del Toro Group is the newly defined Tobabe Formation, the stratoytpe for which is on Little Plantain Cay, an unnamed small island to the west, and along the south coast of Tobabe Point. A basal pebble and cobble conglomerate passes up into an indurated clean quartz and lithic sandstone containing thin volcanic cobble horizons, large sand dollar echinoids, and abundant large thin shelled *Amusium.* Thalassinoid burrow systems, *Ophiomorpha,* and large (10–15 cm in diameter) unidentified shell-filled burrows are very distinctive of this unit. Laterally, the formation contains other mollusks, erect bryozoa, and cross-cutting? tidal channels with coarse volcaniclastic laminated sandstone infilling. By rapid increase in silt and clay content the Tobabe Sandstone grades conformably into the Nancy Point Formation.

The stratotype of the formation runs from Nancy Point to Chong Point but is also well exposed along the south coast of the Valiente Peninsula (Section 15 and in the Toro Cays (Section 14), where it is particularly fossiliferous. The Nancy Point Formation is pervasively bioturbated, shelly, muddy, and silty sandstone with occasional plant fragments and, near the top, a series of channels of coarse volcaniclastic sandstone and fine conglomerate. It ranges in age from 8.2–5.6 Ma and represents bathyal deposition shallowing toward the top.

The Shark Hole Point Formation conformably overlies the Nancy Point Formation (Sections 12, 15) and has its stratotype at the promontory of the same name. The formation is about 200 m thick and consists of micaceous, clayey siltstone that is pervasively bioturbated and contains abundant large scaphopods. The upper part of the formation contains abundant thin shell beds and intraformational slumps with pillow folds and rip-up clasts. The Shark Hole Point is 5.6–3.5 Ma and shows the continuation of the regression begun in the upper Nancy Point Formation.

The Escudo de Veraguas Formation is known only from the island of the same name that lies 27 km east of Nancy Point. It is younger than the Shark Hole Point, ranging in age from 3.5–1.8 Ma, and represents an outer neritic to upper bathyal deposit. Its stratotype, for the lower part of the formation, is along the coast on the east side of the the V-shaped embayment situated in the central part of the north coast, about one kilometer east of Long Bay Point. The stratotype for the upper part of the formation lies along the west coast for about one km. South of Long Bay Point. Lithologically, it consists of pervasively bioturbated clayey siltstone and silty claystone, with frequent concretions, and scattered shelly hash, often with scattered whole and diverse mollusks and ahermatypic corals. The lower part of the formation is more indurated with very common and densely packed cemented burrow concretions and thalassinoid galleries, as well as a distinctive marker bed of corals and mollusks two meters from the base. The upper part of this sequence is capped by a coral biostrome.

The Cayo Agua Formation has its stratotype (Section 19) along the east coast of the island of the same name that lies six km to the west of Toro Point, Valiente Peninsula. Other good exposures of the formation are described in Sections 16, 18, and 20. The Cayo Agua Formation (5.0–3.5 Ma) was deposited in shallower water (inner neritic, 20–40 m) than the coeval Shark Hole Point Formation. Lithologically, the Cayo Agua Formation is distinguished as a pervasively bioturbated, muddy, silty, lithic sandstone with common basalt grains and granules, phosphatic pebbles, and wood fragments. It has many horizons of abundant, diverse, and thick-shelled mollusk asemblages and there is a distinctive marker bed of densely packed ahermatypic corals near the top of the formation, exposed on the coast of Tiburon Point.

The Swan Cay Formation is known only from a small island of the same name, 1.7 km off the north coast of Colon Island. The section is 79 m thick and youngs from south to north across the island. It consists, in the lower part, of shelly calcarenitic siltstone and silty sandstone with coral rubble and red algal fragments. The upper part is formed of massively thick bedded tan-white calcarenite with large *Montastraea* colonies and other corals and mollusks. About 5 m above the base of the calcarenite in large cavities in the calcarenite, deposits of silty, shelly, volcaniclastic sandstone, mixed with volcanic cobbles and boulders, have yielded abundant diverse Pleistocene mollusks and otoliths.

## THE SOUTHERN LIMON BASIN

The Neogene of the southern Limon Basin is represented by the Limon Group, which contains the Uscari, Rio Banano, Quebrada Chocolate, and Moin formations. The name Moin Formations is shown to have priority over the Limon Formation of Bottazzi *et al.* (1994). These formation form a genetically coherent shallowing upward marine sequence that reflects the rise of the Central American isthmus. From the Uscari Formation (oldest; 8.3–5.6 Ma) to the Moin Formation (youngest; ~1.9–1.5 Ma) the depositional environment shallows from bathyal to lagoonal, although one biofacies of the Moin Formation suggests either local upwelling or adjacent deep water.

The basal formation of the Limon group is the Uscari Formation. It consists of a basal 12-m biocalcarenite formed of larger foraminifera and red algal rhodoliths interbedded with foraminiferal, pyroxene-bearing sandstone. The main portion of the formation, about 550 m thick at the stratotype but probably highly variable across the basin, is soft dark gray shale rich in planktic foraminifera. Sections 27 and 28, measured at Sandbox River and Carbon Dos respectively, indicate deposition at bathyal depths, and an age range of 8.3–5.6 Ma, although other parts of the formation may be younger because the transition to the shallow water conditions of the overlying Rio Banano is highly diachronous.

The Rio Banano Formation has its stratotype from Quitaria to Bomba along the banks of the Banano River. Other sections were measured in the Bananito (Section 31), Peje (Section 30), and Vizcaya (Section 39) rivers and the village of Santa Rita (Section 32). Lithologically, the formation at the type locality is dominantly burrow mottled, coarse, tuffaceous, concretionary sandstone with frequent basalt pebbles, leaves, seeds, and wood fragments. Two richly fossiliferous units occur near Quitaria and about 500 m south of Bomba. These are shelly, clayey siltstone and silty sandstone with stringers and lenses of abundant diverse marine mollusks with bryozoa and echinoids at some horizons. Thalassinoid burrow systems are common as are slabby concretionary zones. The Rio Banano Formation is about 750 m thick in its type locality but because of the highly diachronous boundaries with the Uscari and Quebrada Chocolate formations, its thickness varies considerably across the southern Limon Basin. The depositional environment of the formation is inner neritic, close to reef buildups, and it ranges in age from ~3.6–2.8 Ma.

The Quebrada Chocolate Formation, about 500 m. thick at its stratotype (Section 33), has its stratotype along the creek of the same name, immediately west of Buenos Aires, six km west of Limon. The lithology consists of coarse, volcaniclastic, clayey siltstone and sandstone, conglomerate, calcarenite, and reef rubble limestone. Thin low-diversity reef lenses occur in the lower part, and thalassinoid burrow systems and coarsely laminated and cross bedded sandstone characterize the middle part of the formation. The Quebrada Chocolate Formation represents shallow water lagoonal and patch reef depositional environments and ranges in age from 3.5–2.8 Ma. The top of the formation is formed by a distinctive coral reef member, about 140 m thick, whose stratotype is along Route 32 for 1.2 km east of the intersection with Chocolate creek. It consists of a series of coral thickets of *Porites, Acropora, Stylophora, Caulastrea,* and agariciids embedded in a silty clay matrix. The contact with the overlying Moin Formation is either interfingering, with the gray-blue claystone and siltstone, or disconformable with the chanelled Pueblo Nuevo sandstone facies (Taylor, 1975) of the overlying Moin Formation. The Moin Formation is a mosaic of three facies. At the stratotype (Section 37) it consists of blue gray, silty claystone and blocky, clayey, shelly, volcanic sandstone. Basalt granules, scattered mollusks, arthropod burrows are common. Locally, laminated, pyritic and organic rich claystone is present (see upwelling below). In general, the siliciclastic sediments of the Moin Formation are finer than those of the Quebrada Chocolate Formation. The sediments of the stratotype appear to be flank deposits close to associated reef buildups separated below as members of the formation. They may have formed close to local upwelling or down an adjacent, deeper water, shelf slope. The second facies is displayed by the Empalme and Lomas del Mar reef members, which cap the higher ground (about 40 m and above) that lies immediately to the northwest of Limon. The Empalme Member (older) is usually deeply weathered and poorly exposed but contains *Montastraea, Stephanocoenia, Caulastrea, Diploria,* and agariciids in a calcarenite matrix (Section 38).

The Lomas del Mar Member is about 30 m thick (Sections 36, 38) and consists of bioclastic rubbly reef patches, each about 20–50 m in diameter and 1–3 m thick. The unit yields large colonies of *Montastraea cavernosa and Dichocoenia,* small colonies of *Montastraea, Agaricia, Mycetophyllia,* and *Dichocoenia* as well as numerous slender branching colonies of *Madracis asperula.* These reef patches grade into clayey siltstone and calcarenite at their margins, which are packed with small diverse mollusks, including vermetids, as well as oculinid corals, bryozoa, especially cupuladrians, and serpulids. Between the coral reef patches is foraminiferal blue-gray claystone.

The third facies consists of blue-gray siltstone and claystone, extremely rich diverse mollusks, bryozoa, crabs, and oyster beds alternating with tight dark claystone with abundant mangrove root systems, logs, and wood fragments. These sediments are interpreted to represent shallow mangrove and lagoonal seagrass deposits.

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# APPENDIX 1

## Newest Biostratigraphy

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## INTRODUCTION

The Limon and Bocas del Toro groups were first defined and analyzed biostratigraphically by Coates *et al.* (1992). Biostratigraphic determinations for this chapter were made principally by L. Bybell (calcareous nannofossils) and H. Dowsett and M. Cotton (planktic foraminifera). This biostratigraphy is described in detail by Bybell (this volume) and Cotton (this volume). In addition, the Gatun and Chagres formations of the Panama Canal Basin have been extensively revised recently by Collins, Coates, Berggren, Aubry, and Zhang (1996). Subsequent fieldwork has added formations to the Limon and Bocas del Toro groups, and has in some cases revised and expanded the description of the other formations (see Coates, this chapter).

We present here all the biostratigraphic research conducted since Coates *et al.* (1992). The calcareous nannofossil analyses have been done by Aubry and those for planktic foraminifera by Berggren. Calcareous nannofossil and planktic foraminiferal assemblages at most levels are generally scarce, of low diversity, and relatively poorly preserved. This is probably because many of the sections represent relatively near shore, shallow marine deposition. Nevertheless, these collections have allowed us to develop a reliable biozonal assignment for all formations. It has not been possible to recognize precisely any sequence of biostratigraphic datums within zones, thus hampering a precise temporal interpretation of sections (see Aubry, 1995). We use the time scale of Berggren *et al.* (1995).

## NEW FORMATIONS AND SECTIONS OF THE BOCAS DEL TORO GROUP, PANAMA

### The Tobabe Formation

The only samples dated from the Tobabe Sandstone are from Section 14, on the Toro Cays where the formation conformably underlies the Nancy Point Formation but does not expose the unconformable contact with the underlying Miocene volcanics.

Planktic foraminifera occur throughout Section 14 (29 samples) and include *Globigerinoides extremus, G. obliquus, G. trilobus,* and, less frequently, *G. siegliei,* together with the *Globorotalia conomiozea/miotumida* group and the menardine globorotaliids (*G. menardii* "B", *G. pseudomiocenica,* and *G. plesiotumida). Globigerinoides conglobatus* occurs in the lower part of the section and has its FAD near the Miocene/Pliocene boundary. *G. siegliei* is diagnostic of the Late Miocene (Messinian) and Early Pliocene (Zanclian), with a LAD at ~4.7 Ma, and occurs throughout the Tobabe Formation. *Globorotalia plesiotumida* (LAD near the Miocene/Pliocene boundary) occurs throughout the section and *Globorotalia cibaoensis* (LAD at ~ 4.7 Ma) also occurs in one sample. This association strongly suggests that the Tobabe Formation is Late Miocene and largely Messinian (about 7.2–5.3 Ma).

The Chagres Formation, in the Panama Canal Basin, is of comparable age (late Tortonian to Messinian; 8.6–5.3 Ma (Collins *et al.*, 1996) and represents a deepening event from ~25 to 200 meters depositional depth, from the Gatun Formation to the bathyal (200–500 m) basal Toro Member of the Chagres Formation. The Tobabe Formation is the basal, trangressive unit of the Bocas del Toro Group and grades upwards into the Nancy Point Formation, which is also bathyal in origin (Collins, 1993). Correlating the sea level rise represented by the Toro Member and the Tobabe Formation would imply that the base of the Tobabe Formation may be as old as late Tortonian (about 7–8 Ma).

### The Nancy Point Formation;
### Toro Cays and Toro Point Sections

Samples from two new sections of the Nancy Point Formation have been analyzed for both nannofossils and planktic foraminifera. The section on Toro Cays yields common *Discoaster quinqueramus*, indicating Zone NN11 (5.6–8.2 Ma). Planktic foraminifera also suggest Late Miocene (Messinian) and the presence of *Globigerinoides conglobatus,* which normally first appears near the Miocene/Pliocene boundary, and *Globigerinoides siegliei,* which characterizes the Messinian and Zanclian (Early Pliocene), suggests correlation with the upper part of Zone NN11. The younger assignment also agrees with the original biostratigraphic analysis of the Nancy Point Formation (Coates *et al.,* 1992). Section 15, along the westernmost south coast of the Valiente Peninsula, south of Toro Point and west of Playa Verde, includes the Nancy Point Point Formation and contains a fauna that is also assigned to Zone NN11.

### The Cayo Agua Formation

The type section of the Cayo Agua Formation is along the east coast of the island (Section 19) and the oldest units are just south of Norte Point. Planktic foraminifera we have observed include *Globigerinoides obliquus, G. extremus, G. trilobus, Globoquadrina altispira* (LAD at 2.9 Ma), *Globorotalia pseudomiocenica* (LAD at 3.5 Ma), and members of the *N. humerosa/dutertrei* group. This assemblage suggests an early Pliocene age; there are no taxa definitive of the Messinian and there are no specimens of *G. miocenica* whose FAD is at ~3.5 Ma. Our data thus confirm an age of ~5.0–3.5 Ma for the lower Cayo Agua Formation.

The top of the Cayo Agua Formation was poorly constrained by Coates *et al.* (1992) as = or > than 2.9 Ma based on the presence of *Globoquadrina altispira* (LAD at ~2.9 Ma). Work on the nannofossils from PPP 293–301 (Sec. 19) by Bybell (this volume) placed the top of the formation in the upper part of Zone NN15 (3.7–3.8 Ma). From different samples (PPP 348, Sec. 17), we have identified *Discoaster brouweri, D. asymetricus, D. surculus,* and *S. neoabies,* and also note the absence of *Reticulofenestra pseudoumbilicus.* This assemblage would suggest the lowermost Zone NN16 (3.4–3.7 Ma). An age of about 3.4–3.7 Ma seems much more secure than the 2.9 Ma postulated by Coates *et al.* (1992). Section 16 lies on the coast west of Norte Point and contains a lowermost Zone NN16 nannoflora (3.4–3.7 Ma).

### The Swan Cay Formation

A series of samples was examined from the stratotype (Section 25) for both nannofossils and planktic foraminifera. The foraminifera include large, robust specimens of *Globigerinoides ruber, G. conglobatus, G. trilobus* and *Globorotalia truncatulinoides,* and indicate Zone N22 (Lower Pleistocene). One specimen of *Globoturborotalita nepenthes* (LAD at 4.0 Ma) was identified in a sample in the middle of the section. However, no specimens of *Globorotalia pseudomiocenica* or any other diagnostic Pliocene species was found. Furthermore, the nannoflora is extensively reworked, yielding specimens, in various samples, of the Eocene (*e.g., Reticulofenestra reticulata*) as well as *Reticulofenestra pseudoumbilicus, Sphenolithus neoabies, Discoaster* cf. *D. surculus, Ceratolithus cristatus,* and? *Amaurolithus primus,* the last two together characterizing Zones NN13 and NN14 (4.5–3.7 Ma). The large and abundant planktic foraminifera associated with the mollusk faunas in samples PPP 1180 and 1181 seem unequivocally Pleistocene[1], and strongly suggest that the one specimen of *Globoturborotalita nepenthes* is reworked.

## LIMON GROUP, COSTA RICA

### The Rio Banano Formation

The Rio Banano Formation is characterized by the presence of the planktic foraminiferal taxa *Sphaeroidinellopsis subdehiscens* s. str., *Globigerinoides conglobatus* and *Pulleniatina obliquiloculata.* The occurrence of these taxa constrains the age of the Rio Banano Formation to Early Pliocene, ~ 3.5–5.3 Ma. Calcareous nannoplankton taxa include: *Sphenolithus abies* (LAD at ~ 3.6 MA), and *Pseudoemiliania lacunosa* (FAD at ~ 3.7 Ma) in the middle part of the Rio Banano Formation at Quitaria (Coates *et al.,* 1992), and constrains this section to approximately 3.7 to 3.6 Ma in age.

The upper part of the Rio Banano Formation, in the river section at Bomba, contains *Discoaster pentaradiatus* (LAD at 2.46 Ma) and small (<4 μm) *Gephyrocapsa* spp. (FAD at ~3.7 Ma), which constrain the upper part of the formation to Upper Pliocene (Coates *et al.,* 1992). In the immediately overlying and recently exposed landslide section the occurrence of *Globorotalia miocenica* (FAD at 3.5 Ma) and *Dentoglobigerina altispira* (LAD at ~3.1 Ma) constrains the age of the upper part of the Rio Banano Formation more precisely to the early Late Pliocene.

### The Quebrada Chocolate Formation

Microfossils are rare in the newly defined Quebrada Chocolate Formation. A silty clay in Chocolate Creek has yielded small (<0.4 μm) gephyrocapsids, suggesting an age of ~< 3.7 Ma for this unit, consistent with biochronologic estimates of the underlying Rio Banano Formation. Age-diagnostic microfossils are absent in other coral-reef-bearing units.

### The Moin Formation

The presence of large gephyrocapsids (FAD at ~ 1.5 Ma) near the top of Section 34, in Cangrejos Creek, indicate an Early Pleistocene (or younger) for this part of the section. More recent examination of the Cangrejos Creek samples by one of us (MPA) has revealed the presence of small (<0.4 μm) gephyrocapsids (LAD 0.96, FAD 2.5–3.7 Ma) which supports the Lower Pleistocene NN19 assignment by Bybell (this volume), based on G. *truncatulinoides* and *C. macintyrei.*

Large gephyrocapsids (FAD at ~ 1.5 Ma) occur in the lagoonal facies of the Moin Formation (Section 34), flanking the Empalme Member, as does *Globorotalia ungulata,* which is considered a Pleistocene marker.

The Pueblo Nuevo Sandstone of the Limon Formation (McNeill *et al.,* in press), has not yielded unequivocal age-diagnostic microfossils. A latest Pliocene age is estimated on the basis of its stratigraphic position between the underlying Quebrada Chocolate Formation and the overlying reef members of the Moin Formation.

While the reefal Empalme Member has not yielded any age-diagnostic microfossils, Section 34 (west), newly described here, and Section 36 (east), dated by Bybell (this volume) and Cotton (this volume), representing the reefal Lomas del Mar Member, contain biostratigraphically useful microfossils. Section 38 is probably of latest Pliocene to Early Pleistocene age. The lower part of the section contains *P. lacunosa* (LAD at ~0.46 Ma), *C. macintyrei* (LAD at ~1.59 Ma) and *Globigerinoides extremus* (LAD at ~1.8 Ma) which provides a minimum age estimate of 1.8 Ma (or younger). The upper part of the section of the Lomas del Mar Reef Member contains *G. truncatulinoides* (FAD at ~1.9 Ma) and large gephyrocapsids (FAD at ~ 1.5 Ma), suggesting an early Pleistocene (or younger) age. *Gephyrocapsa oceanica,* a form restricted to the Pleistocene, occurs in other samples.

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[1] Editors' note: New paleomagnetic data (D. McNeill, written commun.) indicate pre-Brunhes Chron deposition for collections from Swan Cay, giving an age of Early Pleistocene, 0.78–1.77 Ma.

## CHAPTER 2

# NEOGENE CALCAREOUS NANNOFOSSIL BIOSTRATIGRAPHY OF THE CARIBBEAN COAST OF PANAMA AND COSTA RICA

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## INTRODUCTION

The data presented in this paper are part of the Panama Paleontology Project (PPP) that has as its goal the documentation of the evolutionary and ecological consequences to marine species and environments of the final closure of the Isthmus of Panama (Coates *et al.*, 1992; Collins *et al.*, 1995). This event, which separated the oceanic regimes of the Pacific and the Atlantic, contributed to important climatic, oceanographic, and biologic changes. Calcareous nannofossils were studied from marine deposits in Costa Rica and Panama in order to provide precise biostratigraphic ages for sediments that were deposited before, during, and after the final closure of the Isthmus of Panama. The data presented in this paper were collected by the PPP from 1986 to 1991 and represent the initial results of calcareous nannofossil studies on the Caribbean sections. Other calcareous nannofossil studies in the Caribbean and Gulf of Mexico include Aubry (1993a, 1993b), Gartner *et al.* (1983, 1987), Lang and Watkins (1984), and Watkins and Verbeek (1988). Aubry and Berggren (this volume) review nannofossil work that was undertaken on PPP samples collected from 1991 to 1996. This later work has added new formations to the Limon and Bocan del Toro groups and thus extends and refines the biostratigraphic zonation developed in this first phase of the project. The numbered sections referred to in this chapter are fully described by Coates (Chapter 1 and Appendix B, this volume). Sample numbers refer to the PPP site numbers cataloged in the PPP Database, all of which are also located stratigraphically and geographically by Coates (App. A, B, this volume). The nannofossil occurrence data are available at the internet site http://www.fiu.edu/˜collinsl/.

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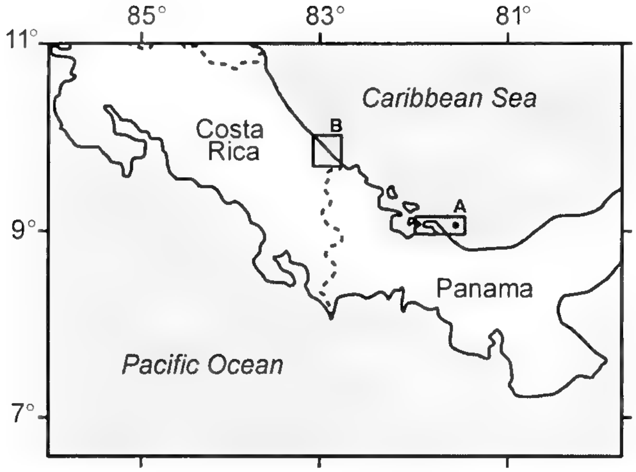
## METHODS

The calcareous nannofossil samples were dried in a convection oven to remove residual water, and the dry sediment was placed in vials for long-term storage in the calcareous nannofossil laboratory at the U. S. Geological Survey in Reston, Virginia. A timed settling procedure was used to obtain the optimum sediment-size fraction. For this procedure, a small amount of sample was placed in a beaker, stirred, and settled through 2 cm of water. An initial settling time of one minute was used to remove the coarse fraction, and a second settling time of 10 minutes was used to remove the fine fraction. Smear slides then were prepared from the remaining suspended material. Cover slips were attached to the slides using Norland Optical Adhesive (NOA-65), a clear adhesive that bonds glass to glass and cures when exposed to ultraviolet light.

Initially, all samples were examined using a Zeiss Photomicroscope III. A few samples, which were thought to have the best preservation and the highest abundances of calcareous nannofossils, were scanned later using a JEOL 35 scanning electron microscope (SEM).

## BIOSTRATIGRAPHIC ZONATION

In this study, the biostratigraphic zonation of the Neogene strata came from 14 composite outcrop sections in Panama and Costa Rica (Text-figs. 1 and 2). The sequence is based primarily upon the calcareous



Text-figure 1.—Map of Panama and Costa Rica showing general location of investigation. A, region in Bocas del Toro Basin that was examined in this study and is enlarged in Text-figure 2A; B, region in Limon Basin that was examined in this study and is enlarged in Text-figure 2B.

nannofossil zonation of Martini (1971), and secondarily upon that of Bukry (1973, 1975, 1978) and Okada and Bukry (1980). There was considerable variation in the abundance and preservation of the calcareous nannofossil assemblages, but they generally were sparse with fair preservation. Most sections contained at least a few barren samples, and some sections had more than half of the samples barren of calcareous nannofossils. However, there were sufficient numbers of specimens, diversity of taxa, and preservational state to allow dating of almost all samples that did contain calcareous nannofossils. Because of the poor preservation in some of the samples, specimens could be identified only to the proper genus (*i.e.*, *Discoaster* sp., *Sphenolithus* sp.).

Table 1 is a list of calcareous nannofossil species that can be used to date sediments of Miocene, Pliocene, and Pleistocene age throughout the world. Not all of these species are present in the study area. Zonal markers for the standard Martini zonation are indicated with an *, and a # indicates a zonal marker for the Bukry zonation. The remaining species have been found to be biostratigraphically useful by various authors. Placement of these additional first appearance datums (FAD's) and last appearance datums (LAD's) within a particular calcareous nannofossil zone is generally accurate, but the relative positions of FAD's and LAD's to each other within an individual zone are much less accurate. Subdivision of Zone NN 19 is from Gartner (1977). Zone NN 19a is used to denote Gartner's *Cyclococcolithina macintyrei* Zone, Zone NN 19b is his *Helicopontosphaera sellii* Zone, Zone NN 19c is his small *Gephyrocapsa* Zone, and Zone NN 19d is his *Pseudoemiliania lacunosa* Zone. Most species in Table 1 are illustrated in Perch-Nielsen (1985). The ages for the FAD's and LAD's are from Berggren *et al.* (1985). Text-figure 3 is a correlation chart from Berggren *et al.* (1985) that has been modified to show only relative placement of calcareous nannofossil zones, planktic foraminiferal zones, epochs, and the geochronometric scale.

## SOUTHERN LIMON BASIN

The southern Limon sedimentary basin is located on the Caribbean (north) coast of Costa Rica near the border with Panama (Text-fig. 1). Samples from seven locations were examined for calcareous nannofossils (Text-fig. 2B). They are Rio Sandbox (Section 27), Carbon Dos (Section 28), Rio Banano (Section 29), Santa Rita (Section 32), Pueblo Nuevo Cemetery (Section 35), Lomas del Mar, Eastern Sequence (Section 36), and Lomas del Mar, Western Reef Flank (Section 37). All the sediments that are exposed at these localities are included in the Limon Group (see Coates *et al.*, 1992; Coates, Chapter 1, this volume).

### LIMON GROUP

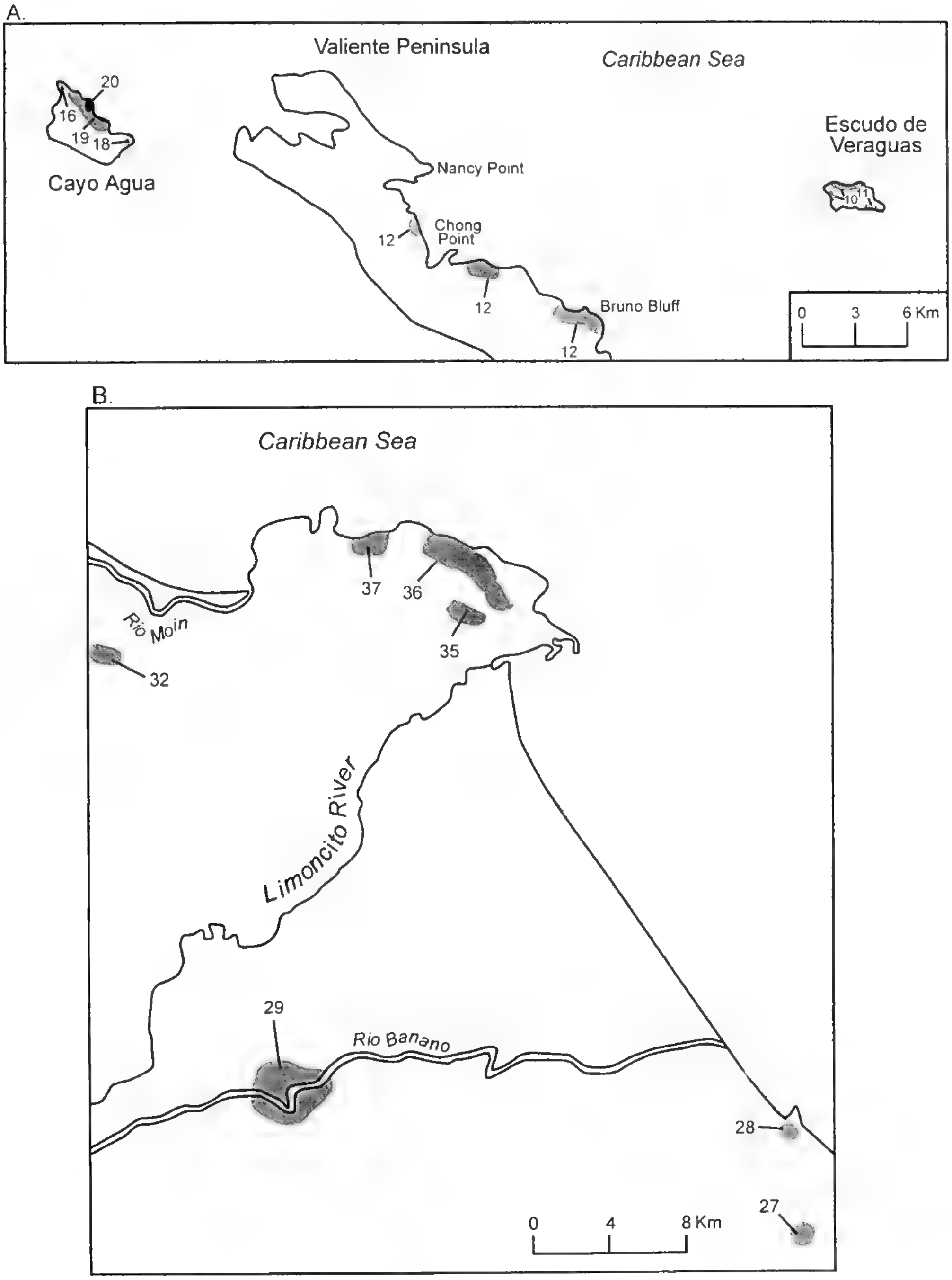
This group consists of the Uscari, Rio Banano, Quebrada Chocolate, and Moin formations, which range from Late Miocene to Late Pleistocene. The lithological descriptions of the formations are given in Coates (this volume).

#### ***Uscari Formation****—Zone NN 11 (Upper Miocene)—8.2–5.6 Ma*

This formation, the oldest in the Limon Group, is at least 565 m thick and consists of biocalcarenite and shale, which in places contains a basaltic sill in its upper part. Calcareous nannofossils were examined from two localities that expose the Uscari Formation: Rio Sandbox (Section 27) and Carbon Dos (Section 28; Text-fig. 2B). Both localities contain calcareous nannofossils that place this formation in the Upper Miocene Zone NN 11 of Martini (1971). See Cotton (this volume) for a discussion of the age of this formation at these two localities based on planktic foraminifera.

#### ***Rio Sandbox locality, Section 27*** *(Zone NN 11)*

Three samples were examined from the upper 20 m of the 40-m-thick section of the Uscari Formation at the Rio Sandbox locality. All three samples are placed in the Upper Miocene Zone NN 11 based on the presence of *Discoaster berggrenii* or *Discoaster quinqueramus*. Both species only occur in Zone NN 11. The following is a list of the species present in each of the



Text-figure 2.—Locations of outcrops in the Bocas del Toro Basin, Panama (A), and in the Limon Basin, Costa Rica (B), that were examined for this study. Numbers refer to assigned section numbers, and more precise geographic positions and composite stratigraphic sections can be found in Appendices A and B, this volume. Map A—10, Escudo de Veraguas, Northern Coast; 11, Escudo de Veraguas, Southeastern Coast; 12, Valiente Peninsula, Bruno Bluff to Plantain Cays; 16, Cayo Agua, North Point, Western Side; 18, Cayo Agua, Piedra Roja Point, Eastern Sequence; 19, Cayo Agua, North Point to Tiburon Point. Map B—27, Rio Sandbox; 28, Carbon Dos; 29, Rio Banano; 32, Santa Rita; 35, Pueblo Nuevo Cemetery; 36, Lomas del Mar, Eastern Sequence; and 37, Lomas del Mar, Western Reef Flank Sequence.

Table 1.—Calcareous nannofossil species useful for dating Miocene, Pliocene, and Pleistocene sediments. * = zonal marker, Martini (1971) zonation. # = zonal marker, Bukry (1973, 1975, 1978) zonation. Ages (Ma) are from Berggren *et al.*, 1985.

| Species | Martini zones | Bukry zones | Age (Ma) |
|---|---|---|---|
| PLEISTOCENE | | | |
| FAD *Emiliania huxleyi* acme | in NN 21 | in CN 15 | 0.085 |
| *#FAD *Emiliania huxleyi* | base NN 21 | base CN 15 | 0.272 |
| *#LAD *Pseudoemiliania lacunosa* | top NN 19d | top CN 14a | 0.474 |
| FAD dominant *Gephyrocapsa* larger | base NN 19d | in CN 14a | |
| LAD dominant *Gephyrocapsa* smaller | top NN 19c | in CN 14a | |
| LAD *Helicosphaera sellii* | top NN 19b | in CN 14a | 1.37 |
| LAD *Calcidiscus macintyrei* | top NN 19a | in CN 14a | 1.45 |
| LAD *Ceratolithus rugosus* | in NN 19a | in CN 14a | |
| #FAD *Gephyrocapsa oceanica* | in NN 19a | base CN 14a | 1.68 |
| #FAD *Gephyrocapsa caribbeanica* | in NN 19a | base CN 13b | 1.74 |
| PLIOCENE | | | |
| FAD *Gephyrocapsa* larger species | in NN 19a | in CN 13a | |
| *#LAD *Discoaster brouweri* | top NN 18 | top CN 12d | 1.9 |
| LAD *Discoaster triradiatus* | mid NN 18 | in CN 12d | 1.9 |
| FAD *Gephyrocapsa aperta* | in NN 18 | in CN 12d | 2.2 |
| LAD *Discoaster asymmetricus* | top NN 17 | top CN 12c | 2.2 |
| *#LAD *Discoaster pentaradiatus* | top NN 17 | top CN 12c | 2.4 |
| *#LAD *Discoaster surculus* | top NN 16 | top CN 12b | 2.4 |
| #LAD *Discoaster tamalis* | upper NN 16 | top CN 12a | 2.6 |
| LAD *Discoaster challengeri* | mid NN 16 | in CN 12a | |
| LAD *Discoaster decorus* | mid NN 16 | in CN 12a | 2.9 |
| LAD *Discoaster variabilis* | mid NN 16 | in CN 12a | 2.9 |
| #LAD *Sphenolithus neoabies* | top NN 15 | top CN 11b | 3.5 |
| LAD *Sphenolithus abies* | top NN 15 | top CN 11b | 3.5 |
| *#LAD *Reticulofenestra pseudoumbilicus* | top NN 15 | top CN 11b | 3.5 |
| FAD *Pseudoemiliania lacunosa* | upper NN 15 | in CN 11a/b | 3.6 modified herein |
| FAD *Discoaster tamalis* | mid NN 15 | in CN 11a/b | 3.8? |
| #LAD *Amaurolithus primus* | top NN 14 | top CN 10d | 3.7 |
| *#LAD *Amaurolithus tricorniculatus* | top NN 14 | top CN 10d | 3.7 |
| *FAD *Discoaster asymmetricus* | base NN 14 | base CN 10d | 4.1 |
| *#FAD *Ceratolithus rugosus* | base NN 13 | base CN 10c | 4.5 |
| #LAD *Ceratolithus acutus* | top NN 12 | top CN 10b | 4.6 |
| #FAD *Ceratolithus acutus* | mid NN 12 | base CN 10b | 5.0 |
| MIOCENE | | | |
| #LAD *Triquetrorhabdulus rugosus* | mid NN 12 | top CN 10a | 5.0 |
| FAD *Helicosphaera sellii* | base NN 12 | base CN 10a | 5.6 |
| *#LAD *Discoaster quinqueramus* | top NN 11 | top CN 9d? | 5.6 |
| LAD *Amaurolithus amplificus* | upper NN 11 | top CN 9c? | 5.6 |
| FAD *Amaurolithus amplificus* | upper NN 11 | base CN 9c? | 5.9 |
| LAD *Discoaster berggrenii* | upper NN 11 | in CN 9b | 5.6 |
| FAD *Amaurolithus tricorniculatus* | upper NN 11 | in CN 9b | 6.0 |
| LAD *Discoaster neohamatus* | upper NN 11 | in CN 9b | |
| FAD *Amaurolithus delicatus* | upper NN 11 | in CN 9b | 6.5 |
| #FAD *Amaurolithus primus* | upper NN 11 | base CN 9b | 6.5 |
| #FAD *Discoaster berggrenii* | base NN 11 | base CN 9a | 8.2 |
| *FAD *Discoaster quinqueramus* | base NN 11 | base CN 9a | 8.2 |
| #FAD *Discoaster surculus* | base NN 11 | base CN 9a | 8.2 |
| LAD *Discoaster bollii* | upper NN 10 | in CN 8b | 8.3 |
| #FAD *Discoaster neorectus* | mid NN 10 | base CN 8b | 8.5 |
| #FAD *Discoaster loeblichii* | mid NN 10 | base CN 8b | 8.5 |
| LAD *Catinaster coalitus* | lower NN 10 | in CN 8a | 9.0 |
| LAD *Catinaster calyculus* | lower NN 10 | in CN 8a | 8.8 |
| LAD *Discoaster exilis* | lower NN 10 | in CN 8a | 8.8 |
| *#LAD *Discoaster hamatus* | top NN 9 | top CN 7b | 8.9 |
| FAD *Discoaster neohamatus* | upper NN 9 | in CN 7b | |
| #FAD *Catinaster calyculus* | in NN 9 | base CN 7b | 10.0 |
| FAD *Discoaster pentaradiatus* | lower NN 9 | in CN 7a | |
| *#FAD *Discoaster hamatus* | base NN 9 | base CN 7a | 10.0 |

Table 1.—Continued.

| Species | Martini zones | Bukry zones | Age (Ma) |
|---|---|---|---|
| *#FAD *Catinaster coalitus* | base NN 8 | base CN 6 | 10.8 |
| FAD *Discoaster challengeri* | mid NN 7 | mid CN 5b | |
| *#FAD *Discoaster kugleri* | base NN 7 | base CN 5b | 13.1 |
| #LAD *Reticulofenestra floridana* | top NN 6 | top CN 5a | 11.6 |
| *#LAD *Sphenolithus heteromorphus* | top NN 5 | top CN 4 | 14.4 |
| FAD *Discoaster variabilis* | base NN 5 | base CN 4 | 16.2 |
| #FAD *Calcidiscus macintyrei* | base NN 5 | base CN 4 | 16.2 |
| *LAD *Helicosphaera ampliaperta* | top NN 4 | top CN 3 | 16.2 |
| #FAD *Sphenolithus heteromorphus* | in NN 4 | base CN 3 | 17.1 |
| *LAD *Sphenolithus belemnos* | top NN 3 | in CN 2 | 17.4 |
| *LAD *Triquetrorhabdulus carinatus* | top NN 2 | in CN 2 | 19.0 |
| #FAD *Sphenolithus belemnos* | in NN 2 | base CN 2 | 21.5 |
| *#FAD *Discoaster druggii* | base NN 2 | base CN 1c | 23.2 |
| FAD *Helicosphaera ampliaperta* | base NN 2 | base CN 1c | 23.2? |
| #LAD *Dicytococcites bisectus* | top NP 25 | top CP 19b | 23.7 |
| *LAD *Helicosphaera recta* | top NP 25 | top CP 19b | |
| #LAD *Sphenolithus ciperoensis* | top NP 25 | top CP 19b | |

samples. Species that are in **bold** are the most useful for dating the samples.

Sample 737 (36.0 m above base of section)

***Discoaster quinqueramus***
*Reticulofenestra pseudoumbilicus*
*Sphenolithus abies*
Abundance: common
Preservation: fair
Age: Zone NN 11

Sample 735 (25.0 m above base of section)

*Calcidiscus macintyrei*
*Helicosphaera carteri*
*Reticulofenestra pseudoumbilicus*
*Sphenolithus abies*
Abundance: common
Preservation: fair
Age: Zone NN 11 by superposition

Sample 736 (21.0 m above base of section)

***Discoaster berggrenii***
*Discoaster brouweri*
*Helicosphaera carteri*
*Reticulofenestra pseudoumbilicus*
*Sphenolithus abies*
Abundance: frequent
Preservation: fair
Age: Zone NN 11

### ***Carbon Dos locality, Section 28*** *(Zone NN 11)*

Two samples were examined from the 15-m-thick section of the Uscari Formation at Carbon Dos, both of which are placed in the Upper Miocene Zone NN 11 based on the presence of *Discoaster berggrenii* and/or *Discoaster quinqueramus*, which only occur within Zone NN 11. The following is a list of the species present in each of the two samples. Species that are in bold are the most useful for dating the samples.

Sample 726 (1.0 m above base of section)

*Calcidiscus leptoporus*
?*Catinaster*
*Coccolithus pelagicus*
***Discoaster berggrenii***
*Discoaster* sp. aff. *D. exilis*
*Discoaster pentaradiatus*
***Discoaster quinqueramus***
*Helicosphaera carteri*
*Reticulofenestra pseudoumbilicus*
*Sphenolithus abies*
Abundance: frequent
Preservation: fair
Age: Zone NN 11

Sample 727 (3.0 m above base of section)

*Calcidiscus macintyrei*
*Coccolithus pelagicus*
***Discoaster berggrenii***
*Discoaster brouweri*
*Discoaster pentaradiatus*
*Helicosphaera carteri*
*Reticulofenestra pseudoumbilicus*
*Reticulofenestra* small species
*Sphenolithus abies*
Abundance: frequent
Preservation: fair
Age: Zone NN 11

### ***Rio Banano Formation****—Zones NN 15–17 (upper Lower to Upper Pliocene)—3.6–2.2 Ma*

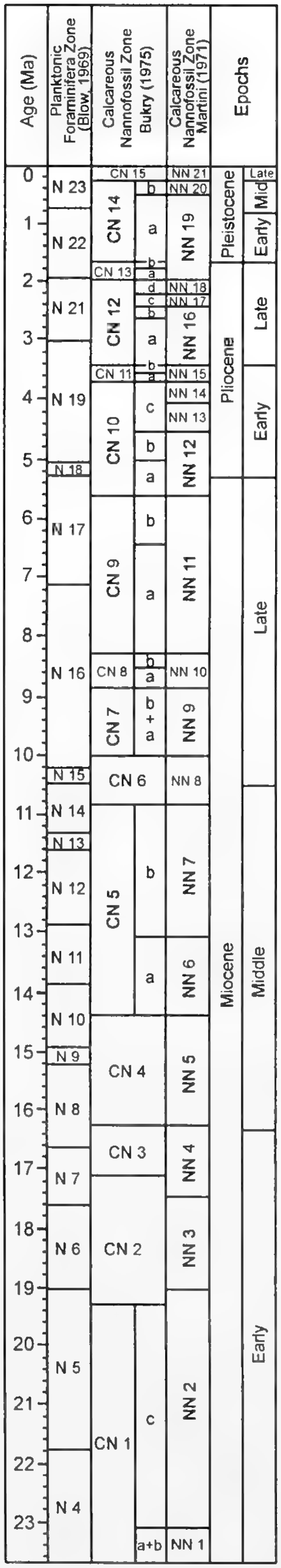
This formation, which overlies the Uscari Formation, can be 750 m thick and consists primarily of siltstone and sandstone. Calcareous nannofossils were examined from two localities: Rio Banano (Section 29) and Santa Rita (Section 32). These sediments can be placed in the upper Lower to Upper Pliocene at Rio Banano and in the Upper Pliocene at Santa Rita, where only the upper part of the formation is exposed.

### *Rio Banano locality, Section 29* (*upper Zone NN 15 to Zone NN 17*)

Twenty-one samples were examined from the 893-m-thick section of the Rio Banano Formation at the Rio Banano locality. Four of these samples were barren of calcareous nannofossils (Text-fig. 4). The lowest 15 samples are placed in the upper part of Zone NN 15 because of the presence in this interval of *Sphenolithus abies*, *Sphenolithus neoabies*, and *Reticulofenestra pseudoumbilicus* (LAD's at the top of Zone NN 15) and *Pseudoemiliania lacunosa* (FAD near the top of Zone NN 15). The overlying samples 672 (789.0 m) and 671 (790.0 m) are probably in Zone NN 16; they do not contain representatives of the genus *Sphenolithus* or the species *R. pseudoumbilicus* (which places them above Zone NN 15) or any smaller representatives of the genus *Gephyrocapsa,* which first appears in Zone NN 17 in the study area. The upper four samples in this section, 670 (791.0 m), 669 (792.5 m), 668 (794.0 m), and 678 (832.5 m), tentatively are placed in Zone NN 17 based on the presence of smaller specimens of the genus *Gephyrocapsa* and specimens of *Discoaster pentaradiatus* (LAD defines the top of Zone NN 17).

### *Santa Rita locality, Section 32* (*Zone NN 16*)

Five samples were examined from the 60-m-thick section of the upper part of the Rio Banano Formation at Santa Rita. The samples from this locality tentatively were placed in Zone NN 16 (Upper Pliocene) (Text-fig. 5). There appears to be some reworking in this section, as evidenced by single specimens of *Reticulofenestra pseudoumbilicus* in samples 721 (38 m) and 720 (58 m) and a single specimen of the genus *Sphenolithus* in sample 723 (13 m). Single occurrences of smaller specimens of the genus *Gephyrocapsa* also occur in samples 723 and 720. If these occurrences are considered to be due to contamination or reworking, these samples may be placed in Zone NN 16 (younger than Zone NN 15 because of the absence of *Sphenolithus* and *Reticulofenestra*



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Text-figure 3.—Correlation of calcareous nannofossil zones, planktic foraminiferal zones, geochronometric scale, and epochs (from Berggren *et al.*, 1985) for the Neogene period.

| 56.0 | 59.0 | 62.0 | 62.5 | 65.0 | 67.5 | 721.0 | 722.0 | 728.5 | 731.0 | 732.5 | 734.5 | 736.0 | 778.0 | 783.5 | 789.0 | 790.0 | 791.0 | 792.5 | 794.0 | 832.5 | Meters Above Base of Section |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Rio Banano Formation | | | | | | | | | | | | | | | | | | | | | Formation |
| Pliocene | | | | | | | | | | | | | | | | | | | | | Series |
| Early | | | | | | | | | | | | | | | Late | | | | | | |
| Upper NN 15 | | | | | | | | | | | | | | | NN 16? | | NN 17 | | | | Calcareous Nannofossil Zone (Martini, 1971) |
| 679 | 680 | 681 | 682 | 683 | 684 | 685 | 686 | 687 | 688 | 689 | 690 | 691 | 677 | 676 | 672 | 671 | 670 | 669 | 668 | 678 | Sample Number / Species |
| | | | | | | | | | | | | | | | | | ● | | | | *Braarudosphaera bigelowii* |
| | | | | ● | | | | | | ● | | ● | | ● | | | | | ● | ● | *Calcidiscus leptoporus* |
| ● | | | | ● | ● | | | | ● | ● | ● | | | | | | ● | | ● | ● | *Calcidiscus macintyrei* |
| ● | | | | | ● | | | | ● | | | ● | | ● | | | | | ● | | *Coccolithus pelagicus* |
| 1 | | | | | | | | | | | | | | | | | | | | | *Cribrocentrum reticulatum* |
| | | | | | | | | | | | | | | | | | | | | ● | *Cyclococcolithus* spp. |
| | | | | | 1 | | | | | | | | | | | | | | | | *Dictyococcites bisectus* |
| | | | | | ● | | | | | | | ● | | | | | | | | | *Discoaster asymmetricus* |
| ● | | | | ● | ● | | | | | ● | ● | ● | | ● | | | | | | ● | *Discoaster brouweri* |
| | | | | | | | | | | | ● | | | | | | | | | | *Discoaster challengeri* |
| | | | | | | | | | | | | | | 1 | | | | | | | *Discoaster deflandrei* |
| ● | | | | | | | | | | ● | ● | | | ● | | | ● | | | ● | *Discoaster pentaradiatus* |
| | | | | | ● | | | | | | | | | | | | | | | | *Discoaster tamalis* |
| | | | | ● | | | | | | | | | | | | | ● | | | ● | *Discoaster* spp. |
| | | | | | | | | | | | 1 | | | | | | ● | | ● | ● | *Gephyrocapsa* smaller species |
| ● | | | | ● | ● | | | | ● | ● | ● | ● | | | | | ● | | ● | ● | *Helicosphaera carteri* |
| | | | | | 1 | | | | | | | | | | | | | | | | *Helicosphaera euphratis* |
| ● | | | | ● | ● | | | | ● | ● | ● | | | | | | ● | | | | *Helicosphaera sellii* |
| | | | | | ● | | | | | | | | | | | | | | | | *Lithostromation operosum* |
| ● | | | | | | | | | | | | | | | | | ● | | | | *Lithostromation perdurum* |
| | | | | | | | | | ● | | ● | | | | | | ● | | | ● | *Pontosphaera discopora* |
| | | | | ● | ● | | | | | | | | | | | | | | ● | | *Pontosphaera* spp. |
| ● | | | | ● | ● | | | | ● | ● | ● | ● | | | | ● | ● | | ● | ● | *Pseudoemiliania lacunosa* |
| | | | | ● | | | | | | | | | | | | | | | | | *Reticulofenestra pseudoumbilicus* |
| | | | | | | | | | | | ● | | | | | | | | | | *Rhomboaster* sp. aff. *R. orthostylus* |
| | | | | | ● | | | | | | | | | | | | | | | | *Scyphospaera amphora* |
| | | | | | | | | | | | | | | | | | ● | | | | *Scyphosphaera apsteinii* |
| ● | | | | ● | ● | | | | ● | ● | ● | | | ● | | | | | | | *Sphenolithus abies* |
| ● | | | | ● | | | | | | | ● | ● | | | | | | | | | *Sphenolithus neoabies* |
| | | | | | | | | | | | | | | | | | 1 | | 1 | | *Sphenolithus* sp. |
| | | | | | ● | | | | | | ● | | | | | | ● | | | ● | *Thoracosphaera* spp. |
| F | R | B | R | F | F | B | B | R | F | F | F | F | B | F | R | F | F | R | C | C | Abundance |
| F | | | | F | F | | | | F | F | F | P | | F | | P | F | | F | F | Preservation |

Text-figure 4.—Calcareous nannofossil occurrences in the Rio Banano Section 29, Costa Rica. See Text-figure 2 for location of exposure. For Text-figures 4–10, the following symbols are used. Abundance: A, abundant or >10 specimens per field of view at ×500; C, common or 1–10 specimens per field of view at ×500; F, frequent or 1 specimen per 1–10 fields of view at ×500; R, rare or 1 specimen for >10 fields of view; B, barren of calcareous nannofossils. Preservation: G, good; F, fair; P, poor. Other symbols: R, specimens likely reworked;? , possible occurrence; numbers, number of specimens observed in the entire sample.

| Rio Banano Formation | | | | | Formation |
|---|---|---|---|---|---|
| Pliocene | | | | | Series |
| Late | | | | | |
| NN 16? | | | | | Calcareous Nannofossil Zone (Martini, 1971) |
| 5.0 | 13.0 | 17.0 | 38.0 | 58.0 | Meters Above Base of Section |
| 709 | 723 | 722 | 721 | 720 | Sample Number / Species |
| | ● | ● | | ● | *Braarudosphaera bigelowii* |
| | ● | | ● | ● | *Calcidiscus leptoporus* |
| | ● | ● | | | *Calcidiscus macintyrei* |
| | | | ● | | *Coccolithus pelagicus* |
| | | ● | | | *Discoaster brouweri* |
| | ● | ● | ● | ● | *Discoaster pentaradiatus* |
| | 1 | | | 1 | *Gephyrocapsa* smaller species |
| ● | ● | ● | ● | ● | *Helicosphaera carteri* |
| | | | | ● | *Pontosphaera discopora* |
| ● | ● | ● | ● | ● | *Pseudoemiliania lacunosa* |
| | | | 1 | 1 | *Reticulofenestra pseudoumbilicus* |
| ● | | | | | *Reticulofenestra* spp. |
| | | | | ● | *Rhabdosphaera clavigera* |
| | 1 | | | | *Sphenolithus* spp. |
| | ● | | | ● | *Thoracosphaera* spp. |
| F | F | F | F | F | Abundance |
| F | F | F | F | F | Preservation |

Text-figure 5.—Calcareous nannofossil occurrences in the Santa Rita Section 32, Costa Rica. See Text-figure 2 for location of exposure and Text-figure 4 for explanation of abundance, preservation, and other symbols.

*pseudoumbilicus*, and older than Zone NN 17 by the absence of smaller specimens of the genus *Gephyrocapsa*). Even if the presence or absence of these three species were discounted, the presence of both *Pseudoemiliania lacunosa* (FAD very near the top of Zone NN 15) and *Discoaster pentaradiatus* (LAD defines the top of Zone NN 17) in these samples confines them to Zone NN 16 or Zone NN 17. See Cotton (this volume) for a discussion of the planktic foraminifera from the Rio Banano locality.

### *Moin Formation—Zone NN 17–19a or b (Upper Pliocene)—2.4–1.7 Ma possibly includes Zone NN 21 (Upper Pleistocene)—2.4–0.275 Ma*

This formation, which overlies the Rio Banano Formation, can be 200 m thick and consists of alternating claystone and sandstone. Calcareous nannofossils were examined from three localities: Pueblo Nuevo Cemetery (Section 35), Lomas del Mar, Eastern Sequence (Section 36), and Lomas del Mar, Western Reef Flank (Section 37) (Text-fig. 2B). Most of the Moin Formation is Upper Pliocene in age, but some Moin sediments may be as young as Upper Pleistocene.

### ***Pueblo Nuevo Cemetery locality, Section 35*** *(Zones NN 17–19)*

Six samples were examined from the 94-m-thick section of the Moin Formation at the Pueblo Nuevo Cemetery. From bottom to top, the samples and their meters above section base include 632 (85.5 m), 631 (89.0 m), 630 (89.5 m), 629 (90.5 m), 628 (90.5 m), and 633 (93.0 m). Five of these samples were barren. Only sample 631 (89.0 m) contained calcareous nannofossils, which indicate either an Upper Pliocene or a Lower Pleistocene age. *Gephyrocapsa* small species first appear in Zone NN 17 in the study area, and *Pseudoemiliania lacunosa* last appears in the upper part of Zone NN 19. The following is a list of the species present in this sample. Species in bold are the most useful for dating the sample.

Sample 631

*Calcidiscus leptoporus*
***Gephyrocapsa* smaller species**
*Helicosphaera carteri*
*Pontosphaera* spp.
***Pseudoemiliania lacunosa***—1 specimen
*Reticulofenestra pseudoumbilicus*—1 specimen (reworked?)
*Thoracosphaera* spp.
Abundance: common
Preservation: fair
Age: upper Pliocene or lower Pleistocene, Zone NN 17–19

### ***Lomas del Mar, Eastern Sequence, Section 36*** *(Zones NN 17/18 or NN 19 and NN 21)*

Thirteen samples were examined from the 70-m-thick composite section of the Moin Formation at Lomas del Mar, Eastern Sequence. This was a difficult section to date because of the large amount of mixing present (Text-fig. 6). There are Late Pliocene to Pleistocene specimens, some obvious Miocene specimens, probably some Oligocene specimens, and a large number of Eocene specimens all occurring in the same samples. If one assumes that reworking is the most likely source for this mixing, then the youngest age present (Late Pliocene to Pleistocene) should reflect the age of deposition for the sediments. However, there are very few of these younger specimens. Only samples 710 (7 m) and 738 (13.5 m) contain specimens of *Gephyrocapsa* larger species (FAD in Zone NN 19). They are absent from the other 11 samples in this sec-

| Moin Formation | | | | | | | | | | | | | Formation |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Pliocene | | | | | | | | | | | | Pleistocene | Series |
| Late | | | | | | | | | | | | Late | |
| NN 17/18 | | | | | | | | | | | | NN21 | Calcareous Nannofossil Zone (Martini, 1971) |
| 7.0 | 12.5 | 13.5 | 14.0 | 22.5 | 24.5 | 30.5 | 31.5 | 33.0 | 34.5 | 36.5 | 38.5 | 65.5 | Meters Above Base of Section |
| 710 | 634 | 635 | 738 | 636 | 637 | 645 | 643 | 642 | 641 | 638 | 640 | 627 | Sample Number / Species |
| | | | | | | | | | ● | | | | Barren |
| ● | | ● | | ● | ● | ● | | | | | ● | | *Braarudosphaera bigelowii* |
| ● | ● | ● | | ● | ● | ● | ● | ● | | ● | ● | | *Calcidiscus leptoporus* |
| | ● | ● | | ● | ● | | | | | | ● | | *Calcidiscus macintyrei* |
| | | | | R | R | | | | | | | | *Catinaster coalitus* |
| | | | | | | ● | | | | | | | *Ceratolithus* spp |
| ● | ● | ● | ● | ● | ● | | | | | | | | *Coccolithus pelagicus* |
| | | | | R | R | | | | | | | | *Cribrocentrum reticulatum* |
| | | | | R | | | | | | | | | *Cyclococcolithus formosus* |
| | | | | R | R | | | | | | | | *Cyclococcolithus neogammation* |
| | | | | R | R | | | | | | | | *Dictyococcites bisectus* |
| | | | | | R | | | | | | | | *Discoaster barbadiensis* |
| | | R | | | R | | | | | | | | *Discoaster berggrenii* |
| | ● | ● | | ● | ● | ● | | | | | ● | | *Discoaster brouweri* |
| | | | | R | R | | | | | | | | *Discoaster challengeri* |
| | | | | R | R | | | | | | | | *Discoaster deflandrei* |
| | ? | | | ● | | | | | | | | | *Discoaster pentaradiatus* |
| 1 | | | | | | | | | | | | | *Discoaster triradiatus?* |
| | | R | | R | | | | | | | | | *Discoaster woodringii* |
| ● | ● | ● | | ● | | ● | | | | | | | *Discoaster* spp |
| | | | | | | | | | | | | ● | *Emiliania huxleyi* |
| | | | | | | | | | | | | ● | *Gephyrocapsa protohuxleyi* |
| 1 | | | ● | | | | | | | | | | *Gephyrocapsa* larger species |
| ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | ● | ● | *Gephyrocapsa* smaller species |
| | | | | | R | | | | | | | | *Helicosphaera bramlettei* |
| ● | ● | | ● | ● | ● | ● | ● | ● | | ● | ● | ● | *Helicosphaera carteri* |
| | | | | R | | | | | | | | | *Helicosphaera compacta* |
| | R | | | R | | | | | | 1 | | | *Helicosphaera euphratis* |
| | | | | ● | | | | | | | | | *Helicosphaera sellii* |
| | | | | R | | | | | | | | | *Markalius inversus* |
| | | | | | R | | | | | | | | *Pentaster lisbonensis* |
| ● | | | | | | | ● | | | | ● | | *Pontosphaera discopora* |
| | ● | | | | ● | | | | | | | | *Pontosphaera multipora* |
| ● | | | | | | ● | | ● | | | | | *Pontosphaera* spp |
| ● | ● | ● | | ● | | ● | ● | ● | | ● | ● | R | *Pseudoemiliania lacunosa* |
| | | | | | | 1 | | | | 1 | | | *Reticulofenestra floridana* |
| | | | | R | | | | | | | | | *Reticulofenestra pseudolockeri* |
| R | R | R | | R | | | | 1 | | | 2 | | *Reticulofenestra pseudoumbilicus* |
| | ● | | | | ● | | | | | | | | *Reticulofenestra* spp |
| ● | | | ● | | | ● | | ● | | | ● | | *Rhabdosphaera clavigera* |
| | | | | | | | | | | ● | | | *Rhabdosphaera* spp. |
| | | | | | | | | ● | | | | | *Scyphosphaera amphora* |
| | R | R | | R | | | | 1 | | | 1 | | *Sphenolithus abies* |
| | | | | | R | | | | | | | | *Sphenolithus tribulosus/predistentus* |
| 1 | | | | | R | | | | | | | | *Sphenolithus* spp |
| | | | ● | | | | | | | | | | *Syracosphaera pulchra* |
| | | | | ● | ● | ● | ● | | | | | | *Thoracosphaera* spp. |
| F | C | C | F | C | F | F | C | F | B | C | F | F | Abundance |
| F | F | F | P | F | F | F | P | F | | F | F | F | Preservation |

Text-figure 6.—Calcareous nannofossil occurrences in the Lomas del Mar, Eastern Sequence Section 36, Costa Rica. See Text-figure 2 for location of exposure and Text-figure 4 for explanation of abundance, preservation, and other symbols.

tion. The presence of the planktic foraminifer *Globorotalia truncatulinoides* (Cotton, this volume) demonstrates an age of <1.9 Ma, which supports placement in calcareous nannofossil Zone NN 19. If this is true, and the *Gephyrocapsa* specimens are in place, then specimens of *Discoaster brouweri* (LAD at top of Zone NN 18), which are found in six of the samples in this section, must be reworked. An alternative choice is to consider *D. brouweri* to be in place and position these samples in either Zone NN 17 or NN 18 based on the presence of smaller specimens of the genus *Gephyrocapsa* (FAD probably in Zone NN 17) and *D. brouweri*.

The highest sample from this section, 627 (65.5 m), was collected from a small construction site just north of the Pueblo Nuevo Cemetery. Akers (1972) examined a sample of the Moin Formation from an outcrop near here, and he placed his sample in the Pleistocene, primarily on the basis of the foraminifera. He found no discoasters in his sample, which he stated could indicate a post-Pliocene age. Sample 627 from the current study, which has been placed tentatively in the Moin Formation, contains *Emiliania huxleyi* (FAD at base of Zone NN 21), and this indicates placement in the uppermost Pleistocene Zone NN 21. The presence of *E. huxleyi* was confirmed with a scanning electron microscope.

### ***Lomas del Mar, Western Reef Flank Sequence, Section 37*** *(Zone NN 19)*

Eleven samples were examined from the 74-m-thick section of the Moin Formation at its type locality at Cangrejos Creek. All eleven samples contained frequent to common calcareous nannofossils with fair to good preservation (Text-fig. 7). There is a minor amount of reworking in this section. The nine lower samples all could be placed in Zone NN 19a because they do not contain *Discoaster brouweri* (LAD defines the top of Zone NN 18) and do contain *Calcidiscus macintyrei* (LAD at the top of Zone NN 19a). The presence of a noticeable amount of larger specimens of the genus *Gephyrocapsa* (FAD in Zone NN 19) in these samples also indicates that they are younger than Zone NN 18. Samples 654 (64 m) and 657 (71 m), the uppermost samples at this locality, each contain only a single specimen of *C. macintyrei* and no *Discoaster* species. If these occurrences are valid, then these samples should be placed in Zone NN 19a. However, if these are reworked specimens, then samples 654 (64 m) and 657 (71 m) should be placed in Zone NN 19b. For the purposes of this paper, these samples are considered to be in either Zone NN 19a or Zone NN 19b. Planktic foraminifera from this locality (Cotton, this volume) indicate an age of 1.8–1.9 Ma, which is consistent with placement of these sediments within Zone NN 19a.

## BOCAS DEL TORO BASIN—PANAMA

The Bocas del Toro sedimentary basin is located on the Caribbean coast of Panama near the border with Costa Rica in the Bocas del Toro Province (Text-fig. 1A). See Coates *et al.* (1992) and Coates (this volume) for a discussion of the geology of this region. Samples from seven locations were examined for calcareous nannofossils (Text-fig. 2B). They are Valiente Peninsula, Bruno Bluff to Plantain Cays (Section 12), Cayo Agua, Punta Norte, Western Side (Section 16), Cayo Agua, Punta Norte to Punta Tiburon (Section 19), Cayo Agua, South of Punta Nispero (Section 20), Cayo Agua, Punta Piedra Roja, Eastern Sequence (Section 18), Escudo de Veraguas Northern Coast (Section 10), and Escudo de Veraguas, Southeastern Coast (Section 11). All of the sediments that were collected from these sections are in the Bocas del Toro Group, first described by Coates *et al.* (1992) and updated by Coates (this volume).

### BOCAS DEL TORO GROUP

This group consists of five formations: the Tobobe Sandstone, the Nancy Point, Shark Hole Point, Cayo Agua, and Escudo de Veraguas formations, Upper Miocene to Upper Pliocene. See Coates, this volume, for lithologic descriptions.

### ***Valiente Peninsula, Bruno Bluff to Plantain Cays locality, Section 12*** *(Zones NN 11–15)*

Eleven samples were examined from the approximately 1,960-m-thick section of the Bocas del Toro Group on the north coast of the Valiente Peninsula. The lower four samples in this section are in the Nancy Point Formation, and the upper seven samples are in the Shark Hole Point Formation. Text-figure 8 is a calcareous nannofossil occurrence chart for this section.

### ***Nancy Point Formation****—Zone NN 11 (Upper Miocene)—8.2–5.6 Ma*

The Nancy Point Formation, the oldest in the Bocas del Toro Group, can be 378 m thick and consists of volcanic sandstone with abundant clay and silt in the matrix. Between the lower three samples of the Nancy Point Formation and the uppermost sample from this formation, there is a thick interval that was not examined for calcareous nannofossils. Sample 409 (1,232 m), the oldest sample examined from this formation, was barren of calcareous nannofossils. Samples 408 (1,236 m), 407 (1,244 m), and 390 (1,606 m) were placed in the Upper Miocene Zone NN 11 because they contain *Discoaster berggrenii* and/or *Dis-*

| Moin Formation | | | | | | | | | | | Formation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Pliocene | | | | | | | | | Early Pleistocene or Late Pliocene | | Series |
| Late | | | | | | | | | | | |
| NN 19a | | | | | | | | | NN 19a/b | | Calcareous Nannofossil Zone (Martini, 1971) |
| 0.5 | 7.0 | 17.0 | 27.0 | 37.0 | 47.0 | 52.5 | 57.0 | 59.0 | 64.0 | 71.0 | Meters Above Base of Section |
| 647 | 648 | 649 | 650 | 651 | 652 | 655 | 653 | 656 | 654 | 657 | Sample Number / Species |
| ● | | | | | | | | | ● | | *Braarudosphaera bigelowii* |
| ● | ● | ● | | ● | | | ● | ● | ● | ● | *Calcidiscus leptoporus* |
| ● | ● | ● | ● | | ● | ● | ● | ● | 1 | 1 | *Calcidiscus macintyrei* |
| | | | | | | | | | ● | | *Ceratolithus* sp. |
| ● | | | | | | | ● | | | | *Coccolithus pelagicus* |
| | | 1 | | | | | | | | | *Cyclococcolithus neogammation* |
| | | | | | | | ● | ● | | | *Cyclococcolithus* spp. |
| 1 | | | | | | | | | | | *Discoaster berggrenii* |
| | | | | | | | 1 | | | | *Discoaster deflandrei* |
| 1 | | | | | | | | | | | *Discoaster* spp. |
| ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | *Gephyrocapsa* larger species |
| ● | ● | ● | | ● | ● | ● | ● | ● | ● | ● | *Gephyrocapsa* smaller species |
| | | | | | | | 1 | | | | *Helicosphaera bramlettei* |
| ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | *Helicosphaera carteri* |
| | ● | ● | | | | | ● | | | ● | *Helicosphaera sellii* |
| | | | | ● | | | | | | | *Lithostromation perdurum* |
| | | ● | | ● | | | | | | ● | *Pontosphaera discopora* |
| | | | | | | | | ● | | | *Pontosphaera millepuncta* |
| | | | | | | ● | | | ● | | *Pontosphaera multipora* |
| | | | ● | | ● | | | | | | *Pontosphaera* spp. |
| ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | *Pseudoemiliania lacunosa* |
| | | | ● | | | | | | | ● | *Rhabdosphaera clavigera* |
| ● | | | | | | | ● | ● | | | *Rhabdosphaera* spp. |
| | | | | | | | | ● | ● | ● | *Scyphosphaera amphora* |
| | | | | | | | | | | ● | *Scyphosphaera apsteinii* |
| | | | ● | | | | | | | | *Scyphosphaera* spp. |
| ● | | | | | | | | | | | *Sphenolithus abies* |
| | | | | | | | 1 | | | | *Sphenolithus* spp. |
| | | | | | | | ● | | | ● | *Syracosphaera pulchra* |
| ● | ● | ● | | | | ● | | | | ● | *Thoracosphaera* spp. |
| F | F | C | F | F | F | F | C | C | F | C | Abundance |
| F | F | F | F | F | G | F | F | F | F | F | Preservation |

Text-figure 7.—Calcareous nannofossil occurrences in the Lomas del Mar, Western Reef Flank Sequence Section 37, Costa Rica. See Text-figure 2 for location of exposure and Text-figure 4 for explanation of abundance, preservation, and other symbols.

| Formation | Nancy Point Formation | | | | Shark Hole Point Formation | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Series | Miocene | | | | Pliocene | | | | | | |
| | Late | | | | Early | | | | | | |
| Calcareous Nannofossil Zone (Martini, 1971) | ? | NN 11 | | | NN 12 | | | | NN 15 | slump NN 12 | ? |
| Meters Above Base of Section | 1232 | 1236 | 1244 | 1606 | 1621 | 1627 | 1639 | 1639 | 1947 | 1948 | 1952 |
| Sample Number / Species | 409 | 408 | 407 | 390 | 388 | 389 | 387 | 386 | 376 | 377 | 378 |
| *Calcidiscus leptoporus* | | | | | | ● | | | ● | | |
| *Calcidiscus macintyrei* | | ● | ● | ● | ● | | | | ● | ● | |
| *Ceratolithus acutus* | | | | | | | ● | | | ● | |
| *Ceratolithus* spp. | | | | | ● | | | | | | |
| *Coccolithus pelagicus* | | | ● | ● | | ● | ● | | | | |
| *Cyclococcolithus* spp. | | | | | | | ● | | | | |
| *Discoaster berggrenii* | | | ● | ● | | | | | | | |
| *Discoaster brouweri* | | | | ● | ● | ● | ● | ● | ● | ● | |
| *Discoaster challengeri* | | | ● | | | | | | | | |
| *Discoaster* sp. aff. *exilis* | | | ● | ● | | | | | | | |
| *Discoaster pentaradiatus* | | ● | ● | ● | ● | ● | ● | ● | ● | ● | |
| *Discoaster quinqueramus* | | ● | ● | | | | | | | | |
| *Discoaster surculus* | | | | ● | | | | | | | |
| *Discoaster variabilis* | | ● | | ● | | | | | | | |
| *Discoaster* spp. | | ● | ● | | ● | | ● | | ● | ● | |
| *Helicosphaera carteri* | | ● | ● | ● | ● | ● | ● | ● | ● | ● | |
| *Helicosphaera euphratis* | | | 1 | | | | | | | | |
| *Helicosphaera lophota* | | | 1 | | | | | | | | |
| *Helicosphaera sellii* | | | | ? | | | ● | | ● | ● | |
| *Markalius inversus* | | | 1 | | | | | | | | |
| *Pontosphaera discopora* | | | | ● | | | | | ● | ● | |
| *Pontosphaera millepuncta* | | | | | | | ● | | ● | | |
| *Pontosphaera multipora* | | | ● | ● | ● | | | | ● | ● | |
| *Pseudoemiliania lacunosa* | | | | | | | | | ● | | |
| *Reticulofenestra pseudoumbilicus* | | ● | ● | ● | ● | | ● | ● | ● | ● | |
| *Reticulofenestra* spp. | | | | | | | ● | ● | | ● | |
| *Rhomboaster* sp. aff. *orthostylus* | | | | | | | | | ● | | |
| *Sphenolithus abies* | | ● | ● | ● | ● | | ● | ● | ● | ● | |
| *Thoracosphaera* spp. | | | | | ● | | ● | | ● | ● | |
| Abundance | B | C | A | C | C | F | C | F | C | C | B |
| Preservation | | F | F | F | F | P | F | P | F | F | |

Text-figure 8.—Calcareous nannofossil occurrences in the Valiente Peninsula, Bruno Bluff to Plantain Cays Section 12, Panama. See Text-figure 2 for location of exposure and Text-figure 4 for explanation of abundance, preservation, and other symbols.

Table 2.—The approximate duration in millions of years for the Neogene NN Zones as presented in Berggren *et al.* (1985). Numbers in parentheses are revised ages from Berggren *et al.* (1995).

| | | | |
|---|---|---|---|
| Zone NN 21—0.275 | (0.26) | Zone NN 10—0.65 | (0.8) |
| Zone NN 20—0.199 | (0.2) | Zone NN 9—1.15 | (1.8) |
| Zone NN 19—1.4 | (1.49) | Zone NN 8—0.8 | (0.6) |
| Zone NN 18—0.3 | (0.5) | Zone NN 7—2.3 | |
| Zone NN 17—0.2 | (0.15) | Zone NN 6—1.3 | |
| Zone NN 16—1.1 | (1.15) | Zone NN 5—1.8 | (2.0) |
| Zone NN 15—0.2 | (0.23) | Zone NN 4—1.2 | (2.7) |
| Zone NN 14—0.4 | (0.19) | Zone NN 3—1.5 | (0.7) |
| Zone NN 13—0.4 | (0.83) | Zone NN 2—4.3 | (4.2) |
| Zone NN 12—1.1 | (0.6) | Zone NN 1—0.5 | (0.7) |
| Zone NN 11—2.6 | (3.0) | | |

*coaster quinqueramus.* Both species only occur in Zone NN 11 (Table 1). This age is consistent with the planktic foraminiferal ages for this formation (Cotton, this volume).

### ***Shark Hole Point Formation****—Zones NN 12–15 (upper Miocene to lower Pliocene)—5.6–3.6 Ma*

Seven samples of the Shark Hole Point Formation were sampled from the north coast of the Valiente Peninsula. The lower part of this section exposes the Nancy Point Formation, while the upper part exposes the Shark Hole Point Formation. Here, the Shark Hole Point Formation can be 341 m thick and consists predominantly of siltstone. Text-figure 8 is an occurrence chart for Valiente Peninsula section. Samples 388 (1,621 m) and 389 (1,627 m), from the lower part of the Shark Hole Point Formation, are placed in Zone NN 12 (Upper Miocene to Lower Pliocene) because they do not contain either *Discoaster berggrenii* or *Discoaster quinqueramus* (the marker species for Zone NN 11), which do occur in the underlying Nancy Point Formation. These samples occur below samples 387 and 386 (both from 1,639 m), which definitely are in Zone NN 12, based on the presence of *Ceratolithus acutus.* Berggren *et al.* (1985) placed the Miocene-Pliocene boundary approximately one-third of the way up into Zone NN 12. Samples 388 and 389 could therefore have been deposited either in the Upper Miocene or the Lower Pliocene. Sample 387 contains *Ceratolithus acutus,* a species that only occurs in the upper part of Zone NN 12 (Lower Pliocene) between 5.0 and 4.6 Ma (Berggren *et al.*, 1985). Sample 386 occurs at the same stratigraphic position as sample 387. Sample 376 (1,947 m) is placed in the upper part of Zone NN 15 (Lower Pliocene) because it contains *Reticulofenestra pseudoumbilicus, Sphenolithus abies* (both have their LAD's at the top of Zone NN 15), and *Pseudoemiliania lacunosa* (FAD near the top of Zone NN 15). Small, poorly preserved, rare, and difficult-to-identify specimens of *P. lacunosa* were described by Rio *et al.* (1990) from farther down in Zone NN 15. They stated that "it becomes abundant and more easily recognizable close to the extinction level of *R. pseudoumbilicus.*" It is this upper horizon with more common and easily identified specimens that is considered significant for this paper.

Sample 377 (1,948 m) was collected from slump material. This is corroborated by calcareous nannofossils because sample 377 contains an almost identical flora to sample 387. Both samples contain the very short ranging species *Ceratolithus acutus* (upper Zone NN 12), and these two samples are presumed to be from the same sedimentary deposit. Sample 378 (1,952 m), the highest sample examined in the section, is barren of calcareous nannofossils. Planktic foraminifera from this location (Cotton, this volume) are able to restrict further the age of this formation to 5.3–3.4 Ma, or the Lower Pliocene.

### ***Cayo Agua Formation****—upper Zone NN 15 (upper lower Pliocene)—3.6–3.5 Ma*

The Cayo Agua Formation either overlies or is a facies equivalent to the upper part of the Shark Hole Point Formation and is in general much coarser. Calcareous nannofossils were examined from this formation at four localities: North Point, Western Side (Section 16), North Point to Tiburon Point (Section 19), South of Nispero Point (Section 20), and Piedra Roja Point, Eastern Sequence (Section 18) (Text-fig. 2B).

### ***Cayo Agua, North Point, Western Side locality, Section 16*** *(upper Zone NN 15)*

Calcareous nannofossils were examined from one sample of the Cayo Agua Formation at the North Point locality. At this site, sample 57, which was collected 49 m above the base of the 50-m-thick section, can be placed in the upper Lower Pliocene in the upper part of Zone NN 15 based on the presence of *Sphenolithus abies* (LAD near the top of Zone NN 15) and *Pseudoemiliania lacunosa* (FAD in the upper part of Zone NN 15). The following is a list of the species present in this sample. Species that are in **bold** are the most useful for dating this sample.

Sample 57 (49 m)

*Calcidiscus macintyrei*
*Discoaster brouweri*
*Discoaster pentaradiatus*
*Helicosphaera carteri*
*Helicosphaera sellii*
*Pontosphaera discopora*
***Pseudoemiliania lacunosa***
*Reticulofenestra* small species

| Cayo Agua Formation Early Pliocene | | | | | | | | | | | | | | | | Formation Series |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| NN 15 | | | | | | | | | | ? | | | | | | Calcareous Nannofossil Zone (Martini, 1971) |
| 45.5 | 46.5 | 48.5 | 50.5 | 150.0 | 174.0 | 200.0 | 230.5 | 247.0 | 264.5 | 268.0 | 271.0 | 279.0 | 288.0 | 289.0 | 291.0 | Meters Above Base of Section |
| 371 | 372 | 373 | 374 | 330 | 324 | 322 | 316 | 331 | 294 | 297 | 301 | 334 | 337 | 336 | 338 | Sample Number / Species |
| | | | ● | | | | | | | | | | | | | *Braarudosphaera bigelowii* |
| ● | | ● | ● | | | | | | ● | | | | | | | *Calcidiscus leptoporus* |
| ● | ● | | ● | | | | | | ● | | | | | | | *Calcidiscus macintyrei* |
| | | ● | | | | | | | | | | | | | | *Ceratolithus rugosus* |
| | | | | | | | | | | | | | | ● | | *Coccolithus pelagicus* |
| | | | | | | | | | | | | | | ● | | *Cyclococcolithus* spp. |
| ● | ● | ● | | | | | | | | | | | | | | *Discoaster brouweri* |
| ● | | ● | ● | | | | | | | | | | | | | *Discoaster pentaradiatus* |
| | | | | | | | | | ● | | | | ● | | | *Discoaster* spp. |
| ● | ● | ● | ● | | ● | | | | ● | | | | | | | *Helicosphaera carteri* |
| R | | | | | | | | | | | | | | | | *Helicosphaera euphratis* |
| | | ● | ● | | | | | | | | | | | | | *Helicosphaera sellii* |
| | | | ● | | | | | | | | | | | | | *Pontosphaera millepuncta* |
| ● | ● | ● | ● | | | | | | | | | | | | | *Pontosphaera multipora* |
| ● | | ● | ● | | | | | | | | | | | | | *Pseudoemiliania lacunosa* |
| ● | ● | ● | ● | ● | | | | | | | | | | | | *Reticulofenestra pseudoumbilicus* |
| ● | ● | ● | ● | | | | | | | | | | | | | *Reticulofenestra* spp. |
| | ● | | | | | | | | | | | | | | | *Rhabdosphaera* spp. |
| | | ● | | | | | | | | | | | | | | *Rhomboaster* sp. aff. *R. orthostylus* |
| ● | ● | ● | ● | | ● | | | | ● | | | | | | | *Sphenolithus abies* |
| | ● | ● | ● | | | | | | | | | | | | | *Thoracosphaera* spp. |
| A | C | C | A | F | R | B | B | B | F | B | B | B | R | R | B | Abundance |
| F | F | F | F | F | F | | | | F | | | | P | P | | Preservation |

Text-figure 9.—Calcareous nannofossil occurrences in the Cayo Agua, North Point to Tiburon Point, Section 19, Panama. See Text-figure 2 for location of exposure and Text-figure 4 for explanation of abundance, preservation, and other symbols.

***Sphenolithus abies***
*Thoracosphaera* spp.
Abundance: common
Preservation: fair
Age: upper Zone NN 15

### *Cayo Agua, North Point to Tiburon Point locality, Section 19 (upper Zone NN 15)*

Sixteen samples from the Cayo Agua Formation were examined for their calcareous nannofossil content from this 293-m-thick section. No samples were examined for calcareous nannofossils from the lowest 45 m of the exposure. Of the 16 samples examined, 7 were barren, and the remaining nine samples contained rare to abundant calcareous nannofossils (Text-fig. 9). Most of the sediments from this section can be placed in calcareous nannofossil Zone NN 15. The co-occurrence of *Reticulofenestra pseudoumbilicus* (LAD at top of Zone NN 15), *Sphenolithus abies* (LAD at top of Zone NN 15), and *Pseudoemiliania lacunosa* (FAD in upper part of Zone NN 15) in these samples indicates that these sediments were deposited near the very top of Zone NN 15. The upper 25 m of this section, however, either was barren of calcareous nannofossils or contained insufficient assemblages for dating.

### *Cayo Agua, South Nispero Point locality, Section 20*

Three samples were examined from this 44-m-thick section: 307 (35.0 m), 305 (36.0 m), and 303 (43.5 m). All three samples were barren of calcareous nannofossils.

### *Cayo Agua, Piedra Roja Point, Eastern Sequence locality, Section 18 (upper Zone NN 15)*

One sample was examined from the 22-m-thick section of the Cayo Agua Formation at the Piedra Roja Point locality. Sample 356, which was collected 5 m above the base of the section, could be placed in the upper part of Zone NN 15 based on the presence of *Sphenolithus abies, Sphenolithus neoabies,* and *Pseudoemiliania lacunosa.* Planktic foraminifera (Cotton, this volume) only could restrict the age of this formation to between 5.3 and 3.5 Ma. The following is a list of species present in this sample. Species that are in **bold** are the most useful for dating this sample.

Sample 356 (5 m)
*Helicosphaera carteri*
***Pseudoemiliania lacunosa***
*Reticulofenestra* small species
***Sphenolithus abies***
***Sphenolithus neoabies***
Abundance: rare
Preservation: fair
Age: upper Zone NN 15

### *Escudo de Veraguas Formation—Zones NN 15 to mid NN 18 (upper Lower to Upper Pliocene)—3.6–2.1 Ma*

### *Escudo de Veraguas, Northern Coast locality, Section 10 (Zones NN 15–18)*

This formation, which probably overlies the Cayo Agua Formation, can be 60 m thick and consists dominantly of claystone and siltstone. Fifteen samples were examined from the 60-m-thick section exposed on the north coast of the island of Escudo de Veraguas. All fifteen samples contained rare to common calcareous nannofossils (Text-fig. 10) and could be placed in a specific calcareous nannofossil zone.

Samples 369 (11.0 m) and 368 (16.5 m), the lowest samples studied from this section, are placed in the upper part of the Lower Pliocene Zone NN 15 by the presence of *Sphenolithus abies* (LAD at the top of Zone NN 15) and *Pseudoemiliania lacunosa* (FAD near the top of Zone NN 15). Overlying samples 367 (21.0 m), 366 (25.5 m), 365 (27.5 m), and 364 (34.5 m) are placed in Zone NN 16 because they contain neither *S. abies* (LAD at top of Zone NN 15) nor smaller species of the genus *Gephyrocapsa* (FAD occurs in Zone NN 17 in the study area). Sample 361 (38.5 m) is placed in Zone NN 17 because it contains *Gephyrocapsa* smaller species and *Discoaster pentaradiatus* (LAD defines the top of Zone NN 17). Samples 363 (40.0 m), 362 (41.5 m), 360 (45.5 m), and 358 (50.5 m) are placed in lower to middle Zone NN 18 based on the absence of *D. pentaradiatus* (LAD defines the top of Zone NN 17) and the presence in sample 358 of *Discoaster brouweri* (LAD at the top of Zone NN 18) and *Discoaster triradiatus* (LAD in middle part of Zone NN 18). Samples 174 (57.7 m), 173 (58 m), 172 (58.6 m), and 171 (59.7 m) also are placed in Zone NN 18 because they overlie samples placed in Zone NN 18 and do not contain larger specimens of *Gephyrocapsa* (FAD in Zone NN 19). Discoasters are absent from these last four samples, except for a few reworked specimens, and, therefore, this genus was not used for age determination in these samples. A minor amount of reworking is present throughout this interval. For example, there is a small amount of material from the Middle to Upper Eocene that is reworked into sample 368. Planktic foraminiferal ages (Cotton, this volume) are consistent with the calcareous nannofossil ages for this formation.

### *Escudo de Veraguas, Southeastern Coast locality, Section 11 (Zones 17–18)*

Three samples were examined from an approximately 20-m-thick section of the Escudo de Veraguas Formation on the south coast of the island of Escudo de Veraguas (Appendix B, this volume). All three samples were collected approximately 11.5 m above the base of the section. This location is away from the type section, and these three samples cannot be located more precisely than being equivalent to some part of the type section. They yield frequent calcareous nannofossils with fair to poor preservation, and they can be placed no more accurately than in uppermost Zone NN 15, Zones NN 16, NN 17, or NN 18 due to the presence of *Discoaster triradiatus* (has its LAD in Zone NN 18) in sample 169 and the presence in all three samples of *Pseudoemiliania lacunosa* (FAD in uppermost part of Zone NN 15). There are few other diagnostic species, although the absence of larger specimens of the genus *Gephyrocapsa* could indicate an age no younger than Zone NN 18. All three samples have some specimens that probably are reworked from older material. If these specimens are discounted, then

| Escudo de Veraguas Formation | | | | | | | | | | | | | | | Formation |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Pliocene | | | | | | | | | | | | | | | Series |
| Early | | Late | | | | | | | | | | | | | |
| NN 15 | | NN 16 | | | | NN 17 | NN 18 | | | | | | | | Calcareous Nannofossil Zone (Martini, 1971) |
| 11.0 | 16.5 | 21.0 | 25.5 | 27.5 | 34.5 | 38.5 | 40.0 | 41.5 | 41.5 | 47.0 | 57.5 | 58.0 | 58.5 | 59.5 | Meters Above Base of Section |
| 369 | 368 | 367 | 366 | 365 | 364 | 361 | 363 | 362 | 360 | 358 | 174 | 173 | 172 | 171 | Sample Number / Species |
| | | | | ● | | ● | | ● | | | | | | | *Braarudosphaera bigelowii* |
| ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | *Calcidiscus leptoporus* |
| | ● | ● | ● | ● | | | | ● | ● | ● | ● | ● | | ● | *Calcidiscus macintyrei* |
| | | | | | | | | | | | | ● | | | *Ceratolithus sp* |
| ● | ● | | | ● | | | | | | | ● | ● | | ● | *Coccolithus pelagicus* |
| | 1 | | | | | | | | | | R | | | | *Cribrocentrum reticulatum* |
| | | | | | | | | | | | | | | 1 | *Cyclococcolithus neogammation* |
| | 1 | | | | | | | | | | | | | | *Dictyococcites bisectus* |
| | ● | | ● | ● | | ● | | | | ● | | | | | *Discoaster brouweri* |
| | | | | | | | | | | | | 1 | | | *Discoaster challengeri* |
| | | | | | | | | | | | | 1 | | | *Discoaster deflandrei* |
| ● | ● | | ● | ● | ● | ● | | | | | | | | | *Discoaster pentaradiatus* |
| | | | | | | | | | | ● | | | | | *Discoaster triradiatus* |
| | | ● | | | | | | | | | | | | ● | *Discoaster* spp |
| | | | | | | ● | | ● | ● | ● | | ● | | ● | *Gephyrocapsa* smaller species |
| ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | *Helicosphaera carteri* |
| | ● | ● | ● | | | | | | | | | | | ● | *Helicosphaera sellii* |
| ● | ● | ● | | ● | | | | | | | | ● | | | *Pontosphaera discopora* |
| | | | ● | | | | | | | | | ● | | | *Pontosphaera multipora* |
| | | | ● | ● | | | | ● | ● | ● | | | | | *Pontosphaera scutellum* |
| | | | | | | | | | | ● | | | | | *Pontosphaera* sp. aff. *P. wechesensis* |
| | | | | | ● | ● | ● | | | | | | | | *Pontosphaera* spp |
| ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | *Pseudoemiliania lacunosa* |
| | 1 | | | | | | | | | | | | | 1 | *Reticulofenestra floridana* |
| | | | | | | | | | | | 1 | | | | *Reticulofenestra pseudoumbilicus* |
| ● | | ● | ● | ● | ● | | ● | | | ● | | ● | | ● | *Reticulofenestra* spp |
| | | | ● | | ● | ● | ● | ● | ● | ● | | | | | *Rhabdosphaera clavigera* |
| | | | ● | | | | | | | | | | | | *Rhabdosphaera* spp |
| | | | | | | | | | | | 1 | | | 1 | *Rhomboaster orthostylus* |
| | ● | | | | | | | | | | | ● | | ● | *Scyphosphaera amphora* |
| | | | | | | ● | | | | | ● | ● | | ● | *Scyphosphaera apsteinii* |
| ● | | | | | | | | | | | | | | | *Scyphosphaera gladstonensis* |
| ● | | | | | | | | | | | | | | | *Scyphosphaera pacifica* |
| | | | | | | | | ● | | | | | | | *Scyphosphaera* spp. |
| ● | ● | | | | | 1 | | | | | 2 | 3 | | 1 | *Sphenolithus abies* |
| | ● | | | | | | | | | | | | | | *Sphenolithus* spp. |
| | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | *Syracosphaera pulchra* |
| | ● | ● | ● | ● | | | | | | ● | ● | ● | | ● | *Thoracosphaera* spp. |
| F | F | F | C | F | F | C | C | C | C | C | F | F | R | F | Abundance |
| F | F | P | F | F | F | F | F | F | F | F | F | F | F | F | Preservation |

Text-figure 10.—Calcareous nannofossil occurrences in the Escudo de Veraguas, Northern Coast Section 10, Panama. See Text-figure 2 for location of exposure and Text-figure 4 for explanation of abundance, preservation, and other symbols.

Table 3.—Summary of calcareous nannofossil ages for each formation.

| Formation | | Epoch | Zone | Age, Ma |
|---|---|---|---|---|
| | | Limon Group | | |
| Moin | | upper Pleistocene to upper Pliocene | NN 17–21 | 2.4–0.275 |
| | or | upper Pliocene | NN 17–19a or b | 2.4–1.7 |
| Rio Banano | | upper Pliocene to upper lower Pliocene | NN 15–17 | 3.6–2.2 |
| Uscari | | upper Miocene | NN 11 | 8.2–5.6 |
| | | Bocas del Toro Group | | |
| Escudo de Veraguas | | upper lower–upper Pliocene | NN 15–mid 18 | 3.6–2.1 |
| Cayo Agua | | upper lower Pliocene | upper NN 15 | 3.6–3.5 |
| Shark Hole Point | | lower Pliocene to upper Miocene | NN 12–15 | 5.6–3.6 |
| Nancy Point | | upper Miocene | NN 11 | 8.2–5.6 |

the samples can be placed in either Zone NN 17 or NN 18.

Sample 168

*Calcidiscus leptoporus*
*Calcidiscus macintyrei*
*Discoaster* spp.—2 specimens (possibly reworked?)
*Helicosphaera carteri*
***Pseudoemiliania lacunosa***
*Reticulofenestra pseudoumbilicus*—1 specimen (reworked?)
*Rhabdosphaera clavigera*
*Rhomboaster orthostylus*—1 specimen (reworked?)
*Sphenolithus abies*—1 specimen (reworked?)
*Syracosphaera pulchra*
*Thoracosphaera* spp.
Abundance: frequent
Preservation: fair
Age: possibly Zone NN 17 or NN 18

Sample 169

*Calcidiscus leptoporus*
*Calcidiscus macintyrei*
*Coccolithus pelagicus*
*Hayaster perplexus*
***Discoaster triradiatus*—1 specimen** (possibly reworked?)
*Gephyrocapsa* smaller species
*Helicosphaera carteri*
*Pontosphaera* sp.
***Pseudoemiliania lacunosa***
*Rhabdosphaera clavigera*
*Scyphosphaera amphora*
*Sphenolithus abies*—3 specimens (reworked?)
*Sphenolithus* sp. aff. *S. radians*—1 specimen (reworked?)
*Syracosphaera pulchra*
*Thoracosphaera* spp.
Abundance: frequent
Preservation: poor
Age: possibly Zone NN 17 or NN 18

Sample 170

*Calcidiscus leptoporus*
*Calcidiscus macintyrei*
*Coccolithus pelagicus*
*Discoaster* sp.—1 specimen (possibly reworked?)
*Gephyrocapsa* smaller species
*Helicosphaera carteri*
*Pontosphaera multipora*
***Pseudoemiliania lacunosa***
*Reticulofenestra pseudoumbilicus*—1 specimen (reworked?)
*Reticulofenestra* sp.
*Rhabdosphaera clavigera*
*Sphenolithus abies*—3 specimens (reworked?)
*Syracosphaera pulchra*
*Thoracosphaera* spp.
Abundance: frequent
Preservation: fair
Age: possibly Zone NN 17 or NN 18

## CONCLUSIONS

Calcareous nannofossils are present, although not abundant, in many exposures along the Caribbean coast of Panama and Costa Rica. The sediments from these outcrops were first described and named by Coates *et al.* (1992), and calcareous nannofossils provided the primary means of determining ages for these marine sediments. Coates *et al.* (1992) divided these formations into two groups: the Bocas del Toro Group for sediments from the northwestern coast of Panama and the Limon Group for sediments from the northern coast of Costa Rica. Table 3 is a summary of the ages for these formations based on calcareous nannofossils.

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## APPENDIX 1

### CALCAREOUS NANNOFOSSIL SPECIES CITED HEREIN

* indicates the presence of the species in Panama or Costa Rica samples

*Amaurolithus amplificus* (Bukry & Percival, 1971) Gartner & Bukry, 1975
*Amaurolithus delicatus* Gartner & Bukry, 1975
*Amaurolithus primus* (Bukry & Percival, 1971) Gartner & Bukry, 1975
*Amaurolithus tricorniculatus* (Gartner, 1967) Gartner & Bukry, 1975
**Braarudosphaera bigelowii* (Gran & Braarud, 1935) Deflandre, 1947
**Calcidiscus leptoporus* (Murray & Blackman, 1898) Loeblich & Tappan, 1978
**Calcidiscus macintyrei* (Bukry & Bramlette, 1969) Loeblich & Tappan, 1978
*Catinaster calyculus* Martini & Bramlette, 1963
**Catinaster coalitus* Martini & Bramlette, 1963
**Ceratolithus acutus* Gartner & Bukry, 1974

*Ceratolithus rugosus* Bukry & Bramlette, 1968
**Coccolithus pelagicus* (Wallich, 1877) Schiller, 1930
**Cribrocentrum reticulatum* (Gartner & Smith, 1967) Perch-Nielsen, 1971
**Cyclococcolithus formosus* Kamptner, 1963
**Cyclococcolithus neogammation* Bramlette & Wilcoxon, 1967
**Dictyococcites bisectus* (Hay, Mohler, & Wade, 1966) Bukry & Percival, 1971
**Discoaster asymmetricus* Gartner, 1969
**Discoaster barbadiensis* Tan Sin Hok, 1927
**Discoaster berggrenii* Bukry, 1971
*Discoaster bollii* Martini & Bramlette, 1963
**Discoaster brouweri* Tan Sin Hok, 1927
**Discoaster challengeri* Bramlette & Riedel, 1954
*Discoaster decorus* Bukry, 1973
**Discoaster deflandrei* Bramlette & Riedel, 1954
*Discoaster druggii* Bramlette & Wilcoxon, 1967
**Discoaster exilis* Martini & Bramlette, 1963
*Discoaster hamatus* Martini & Bramlette, 1963
*Discoaster kugleri* Martini & Bramlette, 1963
*Discoaster loeblichii* Bukry, 1971
*Discoaster neohamatus* Bukry & Bramlette, 1969
*Discoaster neorectus* Bukry, 1971
**Discoaster pentaradiatus* Tan Sin Hok, 1927
**Discoaster quinqueramus* Gartner, 1969
**Discoaster surculus* Martini & Bramlette, 1963
**Discoaster tamalis* Kamptner, 1967
**Discoaster triradiatus* Tan Sin Hok, 1927
**Discoaster variabilis* Martini & Bramlette, 1963
**Discoaster woodringii* Bramlette & Riedel, 1954
**Emiliania huxleyi* (Lohmann, 1902) Hay & Mohler *in* Hay and others, 1967
*Gephyrocapsa aperta* Kamptner, 1963
*Gephyrocapsa caribbeanica* Boudreaux & Hay, 1969
*Gephyrocapsa oceanica* Kamptner, 1943
**Gephyrocapsa protohuxleyi* McIntyre, 1970
**Hayaster perplexus* (Bramlette & Riedel, 1954) Bukry, 1973
*Helicosphaera ampliaperta* Bramlette & Wilcoxon, 1967
**Helicosphaera bramlettei* (Müller, 1970) Jafar & Martini, 1975
**Helicosphaera carteri* (Wallich, 1877) Kamptner, 1954
**Helicosphaera compacta* Bramlette & Wilcoxon, 1967
**Helicosphaera euphratis* Haq, 1966
**Helicosphaera lophota* (Bramlette & Sullivan, 1961) Locker, 1973
*Helicosphaera recta* (Haq, 1966) Jafar & Martini, 1975
**Helicosphaera sellii* (Bukry & Bramlette, 1969) Jafar & Martini, 1975
**Lithostromation operosum* (Deflandre *in* Deflandre and Fert, 1954) Bybell, 1975
**Lithostromation perdurum* Deflandre, 1942
**Markalius inversus* Bramlette & Martini, 1964
**Pentaster lisbonensis* Bybell & Gartner, 1972
**Pontosphaera discopora* Schiller, 1925
**Pontosphaera japonica* (Takayama, 1967) Nishida, 1971
**Pontosphaera multipora* (Kamptner *ex* Deflandre, 1959) Roth, 1970
**Pontosphaera scutellum* Kamptner, 1952
**Pontosphaera wechesensis* (Bukry & Percival, 1971) Aubry, 1986
**Pseudoemiliania lacunosa* (Kamptner, 1963) Gartner, 1969
**Reticulofenestra floridana* (Roth & Hay *in* Hay *et al.*, 1967) Theodoridis, 1984
**Reticulofenestra pseudolockeri* Jurasova, 1974
**Reticulofenestra pseudoumbilicus* (Gartner, 1967) Gartner, 1969
**Rhabdosphaera clavigera* Murray & Blackman, 1898
**Rhomboaster orthostylus* (Shamrai, 1963) Bybell & Self-Trail, 1995
**Scyphosphaera amphora* Deflandre, 1942
**Scyphosphaera apsteinii* Lohmann, 1902
**Scyphosphaera gladstonensis* Rade, 1975
**Scyphosphaera pacifica* Rade, 1975
**Sphenolithus abies* Deflandre *in* Deflandre and Fert, 1954
*Sphenolithus belemnos* Bramlette & Wilcoxon, 1967
*Sphenolithus ciperoensis* Bramlette & Wilcoxon, 1967
*Sphenolithus heteromorphus* Deflandre, 1953
**Sphenolithus neoabies* Bukry & Bramlette, 1969
**Sphenolithus predistentus* Bramlette & Wilcoxon, 1967
**Sphenolithus radians* Deflandre *in* Grassé, 1952
**Sphenolithus tribulosus* Roth, 1970
**Syracosphaera pulchra* Lohmann, 1902
*Triquetrorhabdulus carinatus* Martini, 1965
*Triquetrorhabdulus rugosus* Bramlette & Wilcoxon, 1967

# CHAPTER 3

# NEOGENE PLANKTIC FORAMINIFERAL BIOCHRONOLOGY OF THE SOUTHERN CENTRAL AMERICAN ISTHMUS

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## INTRODUCTION

It has been sixty years since Thalman (1934) pioneered the use of planktic foraminifera for interregional correlation, illustrating their biostratigraphic utility. Early applications of planktic foraminifera in biostratigraphy occurred in three primary regions: the Alpine-Mediterranean region, Russia, and Trinidad, in the Caribbean Basin (Bolli, 1974). Since then, planktic foraminifera have proven valuable in providing age constraints on marine deposits around the world, both in land-based sections and in deep-sea cores.

This study is part of the Panama Paleontology Project and the first major study of the planktic foraminifera on the southern Central American isthmus (Cotton, 1990, 1991). The study area includes the Caribbean coast of Costa Rica and Panama, specifically the Limon and Bocas del Toro basins (Appendix A, Maps 4–11). The purpose of the study is to provide a precise biochronologic framework for the stratigraphic units which encompass the Pliocene emergence of the isthmus. Detailed biostratigraphic data offer age constraints needed to resolve the tectonic history of the isthmus, in particular, the timing of emergence.

Another product of this study is a Neogene stratigraphic correlation scheme for the Caribbean Basin based on data from planktic foraminiferal studies in Mexico (both Pacific and Caribbean coasts), Venezuela, Colombia, Equador, St. Croix, Dominican Republic, Jamaica, Puerto Rico, Florida, Virginia, North and South Carolina, and the Pacific coasts of Panama and Costa Rica. In some instances re-evaluation of earlier studies was necessary prior to correlation.

## ACKNOWLEDGMENTS

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## METHODS

Seventy-five samples collected from ten locales were utilized in this study. Approximately fifty grams from each sample were disaggregated by soaking in water, and heated on a hot plate for several hours. If the sample proved difficult to dissaggregate, one of two methods was employed: (1) soaking the sample overnight in a solvent (such as paint thinner, kerosene or turpentine), followed by soaking it in water and heating; (2) adding Quaternary-O (a petroleum byproduct) and heating in water (Zangula, 1968). Following disaggregation, the samples were washed through <850 μm and >63 μm nested sieves to concentrate the fraction larger than silt. The > 850 μm and < 63 μm portions were discarded. The remaining fraction was transferred to filter paper and oven dried at ~50°C. From a representative split of each sample, all planktic foraminifera (usually >200 specimens) were picked and identified to the species level following the taxonomy of Kennett and Srinivasan (1983) and Bolli and Saunders (1985). Additional comparisons were made with specimens housed in the Cushman Collection, which resides in the U. S. National Museum of Natural History, Smithsonian Institution, Washington, D.C. In samples with abundant specimens, planktic foraminifera were picked from random squares on the picking tray until 300 specimens were obtained. All identifications were made by the author.

## BIOSTRATIGRAPHY

Thirty-nine species of planktic foraminifera were identified in the Neogene deposits along the Caribbean coast of western Panama and eastern Costa Rica (Tables 1, 2). In general, the planktic foraminifera were both abundant and well preserved with the notable exception of the Rio Banano Formation, in which they were sparse and poorly preserved. Total faunal diversity (number of planktic foraminifer species per sample) varied from 2 to 20 and mean species diversity varied from 7 to 16 in the formations studied. Stratigraphic ranges of last appearance datums ("LADs")

Table 1.—Faunal list.

*Candeina nitida* d'Orbigny, 1939
*Dentogloboquadrina altispira* (Cushman and Jarvis), 1936
*Globigerina apertura* Cushman, 1918
*Globigerina bulloides* (d'Orbigny), 1826
*Globigerina decoraperta* Takayanagi and Saito, 1962
*Globigerina falconensis* Blow, 1959
*Globigerina nepenthes* Todd, 1957
*Globigerina woodi* Jenkins, 1960
*Globigerinella aequilateralis* (Brady), 1879
*Globigerinella calida* (Parker), 1962
*Globigerinita glutinata* (Egger), 1893
*Globigerinoides conglobatus* (Brady), 1879
*Globigerinoides obliquus* Bolli, 1957
*Globigerinoides obliquus* Bolli, var. *extremus* Bolli and Bermudez, 1965
*Globigerinoides ruber* (d'Orbigny), 1839
*Globigerinoides sacculifer* Brady, 1877
*Globigerinoides seigliei* Bermudez and Bolli, 1969
*Globorotalia crassaformis* (Galloway and Wissler), 1927
*Globorotalia exilis* Blow, 1969
*Globorotalia juanai* Bermudez and Bolli, 1969
*Globorotalia margaritae* Bolli and Bermudez, 1965
*Globorotalia menardii* (Parker, Jones and Brady), 1865
*Globorotalia miocenica* Palmer, 1945
*Globorotalia plesiotumida* Blow and Banner, 1965
*Globorotalia pseudomiocenica* Bolli and Bermudez, 1965
*Globorotalia puncticulata* (Deshayes), 1832
*Globorotalia scitula* (Brady), 1882
*Globorotalia tosaensis* Takayanagi and Saito, 1962
*Globorotalia truncatulinoides* (d'Orbigny), 1839
*Globorotalia tumida* (Brady), 1877
*Orbulina universa* d'Orbigny, 1839
*Neogloboquadrina acostaensis* (Blow), 1959
*Neogloboquadrina dutertrei* (d'Orbigny), 1839
*Neogloboquadrina humerosa* (Takayanagi and Saito), 1962
*Neogloboquadrina pachyderma* (Ehrenberg), 1861
*Pulleniatina obliquiloculata* (Parker and Jones), 1865
*Pulleniatina primalis* Banner and Blow, 1967
*Sphaeroidinella dehiscens* (Parker and Jones), 1865
*Sphaeroidinellopsis seminulina* (Schwager), 1866
*Turborotalita quinqueloba* Natland, 1938

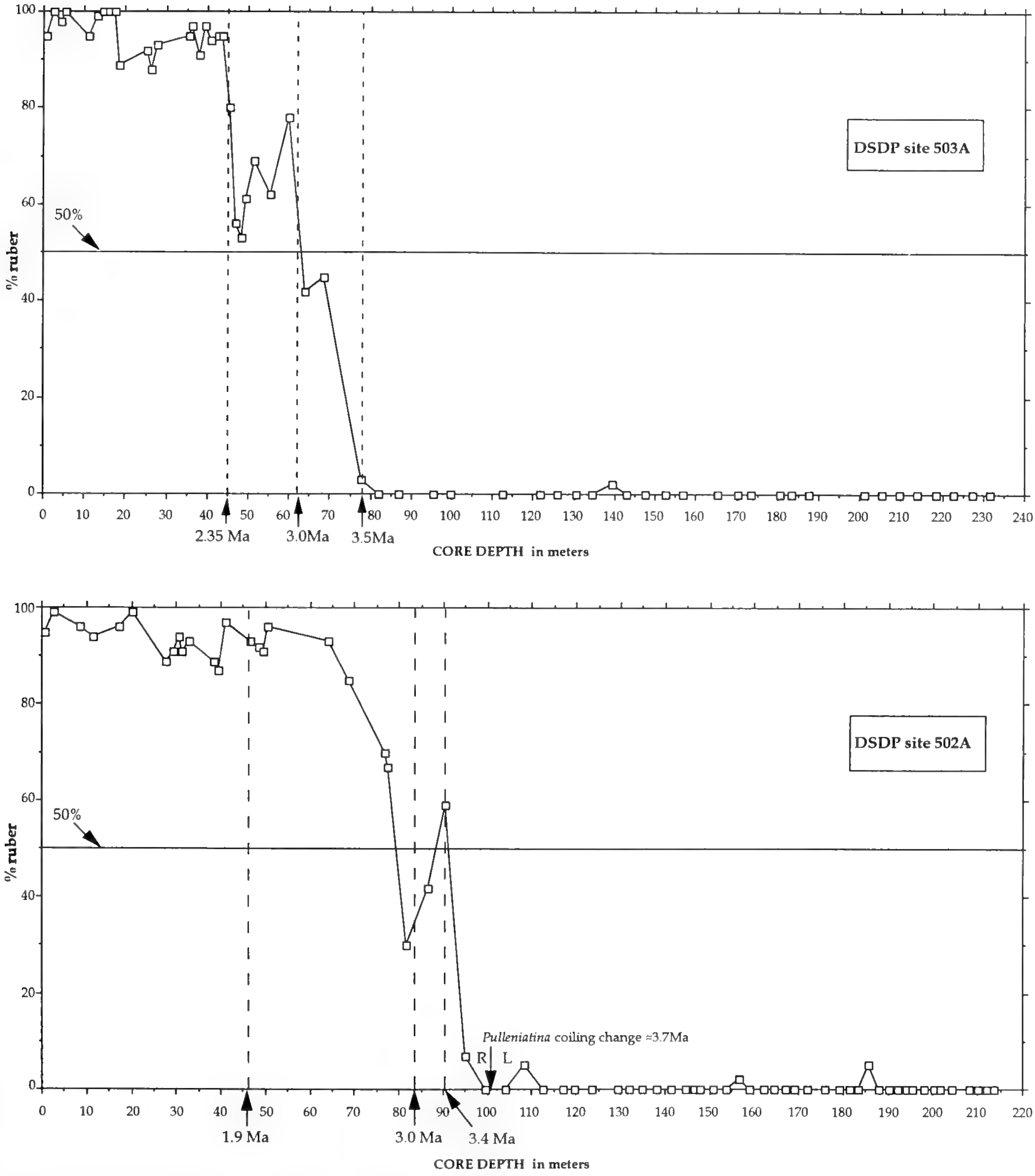
Text-figure 1.—Map of the Americas showing locations of land-based Neogene sediments and Deep Sea Drilling Project (DSDP) sites containing planktic foraminifera and discussed in text.

and first appearance datums ("FADs") of planktic foraminifer species identified in this study (Table 3) are taken from Bolli and Saunders (1985) and Dowsett (1989).

Bolli and Saunders (1985) document *Globigerinoides ruber* originating in the Early Miocene and disappearing from the fossil record between the late Middle Miocene to within the Early Pliocene (approximately 11.3–5.1 Ma), the so-called "*ruber*-gap". However, based on data from Keller *et al.* (1989) on DSDP site 503A (Pacific side of the Central American isthmus, Text-fig. 1), and DSDP site 502A (Caribbean side of the Central American isthmus), *G. ruber* is missing from the fossil record from the base of both cores (Late Miocene) to approximately 3.5 Ma (Text-fig. 2). *Globigerinoides ruber* increases in number and percentage relative to *G. obliquus* to approximately 2.0 Ma, when *G. ruber* outnumbers *G. obliquus* about 9 to 1 (*G. ruber* ratio = 0.9) . The relatively rapid turnover from a *G. obliquus*-dominated to a *G. ruber*-dominated fauna simultaneously in both cores is remarkable and led to the use of a value called "percent *ruber*" ( = *G. ruber*/*G. ruber* + *G. obliquus* × 100). It also suggests an oceanic connection between the Caribbean and the Pacific at that time (3.5 Ma). *Globigerinoides obliquus* in this study includes *G. extremus,* which is considered a morphologic variant of *G. obliquus,* although many planktic foraminiferal workers recognize a unique FAD for *G. extremus* in the Late Miocene.

Previous studies of calcareous microfossils from the southern Central American isthmus include Cushman, 1918; Coryell and Mossman, 1942; Jenkins, 1964; Bold, 1967a, 1967b, 1972; Blacut and Kleinpell, 1969; Bandy, 1970; Akers, 1972; Taylor, 1975; Cassell, 1986; Pizarro, 1987; Berrangé *et al.*, 1989; Cassell and Sen Gupta, 1989a, 1989b; Corrigan *et al.,* 1990; and Duque-Caro, 1990. Generally, these studies were limited to a single formation and, for the most part, involved age determinations based on correlation to conventional calcareous microfossil zonations. There has been no comprehensive biostratigraphic work done for the Neogene deposits from the southern Central American isthmus until this study (see Cotton, 1991, for original biostratigraphic data).

All calcareous nannofossil data used in this chapter



Text-figure 2.—Plot of percent *Globigerinoides ruber* relative to *G.obliquus* for DSDP sites 502A (Caribbean) and 503A (Pacific) versus core depth (m), based on data from Keller *et al.* (1989).

Table 2.—Occurrences of planktic foraminifera at PPP sites (numbered across top). Numbers are in stratigraphic order from top = left, to bottom = right. Samples from the same section (App. B) are joined with a "-". Data are available at internet site http://www.fiu.edu/˜collinsl/.

| | Uscari Fm. | | | | St. Rita | | | Rio Banano Fm. | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 726 | 737 | -735 | -736 | 720 | -721 | 700 | 678 | -668 | -670 | -672 | -690 | -689 | -688 | -687 | -686 | -685 | -684 | -683 | -682 | -679 |
| *Candeina nitida* | | | | | | | | | | | | | | | | | | | | | |
| *Dentoglobоquadrina altispira* | x | x | x | x | x | | x | | | | | x | x | x | | x | x | | x | x | |
| *Globigerina apertura* | x | | | | x | | x | x | x | x | x | | x | x | x | | | | | | |
| *Globigerina bulloides* | x | | | x | x | x | | x | x | x | x | | x | x | | x | | | | x | x |
| *Globigerina decoraperta* | x | | x | x | | | | x | | | | | | | | x | x | | | x | |
| *Globigerina falconensis* | | | | | x | | | | | x | | | x | | | | | | | x | x |
| *Globigerina nepenthes* | | | | x | | | | | | | | | | | | | | | | | |
| *Globigerina woodi* | | | | x | | | | x | x | | | | | | | | | | | | |
| *Globigerinella aequilateralis* | | x | x | x | x | x | x | x | x | x | | | | x | | | | | | | |
| *Globigerinella calida* | | | | | | | | | | | | | | | | | | | | | |
| *Globigerinita glutinata* | | | | x | | | | x | x | | | x | | | | | | | | | x |
| *Globigerinoides conglobatus* | x | | | | | x | | | x | | | | | | | | | | | | |
| *Globigerinoides obliquus* | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | | | x | x |
| *Globigerinoides ruber* | | | | | x | x | | x | x | x | x | x | x | x | | | | x | x | x | |
| *Globigerinoides sacculifer* | x | x | x | x | x | x | x | x | x | x | x | x | x | x | | x | x | x | x | | x |
| *Globigerinoides seigliei* | | | | | | | | | | | | | | | | | | | | | |
| *Globorotalia crassaformis* | | | | | x | | | | | | | | | | | | | | | | |
| *Globorotalia exilis* | | | | | | | | | | | | | | | | | | | | | |
| *Globorotalia juanai* | x | | | | | | x | | | | | | | | | | | | | | |
| *Globorotalia margaritae* | | | | | | | | | | | | | | | | | | | | | |
| *Globorotalia menardii* | x | | x | | x | x | x | | | x | | | | | | | | | | | |
| *Globorotalia miocenica* | | | | | | | | | | | | | | | | | | | | | |
| *Globorotalia plesiotumida* | x | x | x | x | x | | | x | x | | | | | x | | x | x | x | | | x |
| *Globorotalia pseudomiocenica* | | | | | | | | | | | | | | | | | | | | | |
| *Globorotalia puncticulata* | | | | | | | | | | | | | | | | | | | | | |
| *Globorotalia scitula* | x | | | | | | x | | | | | | | | | | | | | | |
| *Globorotalia tosaensis* | | | | | | | | | | | | | | | | | | | | | |
| *Globorotalia truncatulinoides* | | | | | | | | | | | | | | | | | | | | | |
| *Globorotalia tumida* | | | | | | | | | | | | | | | | | | | | | |
| *Neogloboquadrina acostaensis* | x | | x | | | x | x | x | | x | | | | | | | x | | | | x |
| *Neogloboquadrina dutertrei* | | | | | | | | | x | | | | | | | | | | | | |
| *Neogloboquadrina humerosa* | | | | | x | x | | x | | | | | x | x | | | | | | | |
| *Neogloboquadrina pachyderma* | | | | | | | | | | | | | | | | | | | | | |
| *Orbulina universa* | x | x | x | x | | | x | | | x | | | x | x | | | | | | | |
| *Pulleniatina obliquiloculata* | | | | | | | | | | | | | | | | | | | | | |
| *Pulleniatina primalis* | | | | | | | | | | | | | | | | | | | | | |
| *Sphaeroidinella dehiscens* | | | | | | | | | | | | | | | | | | | | | |
| *Sphaeroidinellopsis* sp. | | | x | x | | | x | | | | | | | | | | | | | | |
| *Turborotalia quinqueloba* | | | | | | | | | | | | | | | | | | | | | |

are by the courtesy of L. Bybell, U. S. Geological Survey, who provided the identifications of the nannofossils for the initial part of the Panama Paleontology Project (Chapter 2, this volume). Nannofossil data from the isthmus are used to support, or show conflict with, the planktic foraminifera-based age constraints.

## LIMON GROUP

The Limon Group deposits occur in the Limon Basin along the southeastern Caribbean coast of Costa Rica (Appendix A, Maps 10–11) with exposure south and west of the town of Limon. The Limon Basin contains approximately 10,000 meters of marine sediments ranging from Paleocene to Pleistocene in age (Weyl, 1980). The Limon Group represents the Neogene portion of these deposits and is comprised of the Uscari, the Rio Banano and the Moin formations, totaling over 1500 m of sediment. These Neogene sediments were deposited in a back-arc setting behind the uplifted Cordillera de Talamanca (Galli-Olivier, 1979; Escalante, 1990).

The earliest published reference to these deposits was by Gabb (1895), who coined the term "Moin Clay Member" and described the molluscan fauna in the Limon region. Hill (1898) also made reference to fossils collected in the Limon area during his reconnaissance of the isthmus. Nearly a quarter of a century later, Olsson (1922) collected and described mollusks from the Limon area and named the Uscari Formation after the Uscari creek about 50 km south of Limon.

Table 2.—Extended.

| | Moin Fm. | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 631 | 638 | 643 | 645 | 637 | 636 | 635 | 710 | 658 | 657 | 654 | 656 | 653 | 655 | 652 | 650 | 648 | 647 | 705 | 712 |
| *Candeina nitida* | | | | | | | | | | | | | | | | | | | | |
| *Dentogloboquadrina altispira* | | | | | | | | | | | | | | | | | | | | |
| *Globigerina apertura* | | x | | | | | | | | | | | | | | | | | | x |
| *Globigerina bulloides* | | | | | | | | | | | | | | x | | | | | | |
| *Globigerina decoraperta* | | | | | x | | | | | | | | | | | | x | | | |
| *Globigerina falconensis* | | | | | | | | | | x | | | | | | | | | | |
| *Globigerina nepenthes* | | | | | | | | | | | | | | | | | | | | |
| *Globigerina woodi* | | | | | | | | | | | | | | | | | | | | x |
| *Globigerinella aequilateralis* | x | | x | x | | x | x | x | | | | | | x | | | | | | |
| *Globigerinella calida* | | | | | | | | | | | | | | | | | | | | |
| *Globigerinita glutinata* | | x | x | | | x | | | | | | | | x | | | x | | | x |
| *Globigerinoides conglobatus* | x | | | x | | | | x | x | | | x | x | x | x | x | | | | |
| *Globigerinoides obliquus* | | | | | | | | | x | x | | | | | | x | | | x | |
| *Globigerinoides ruber* | x | x | x | x | x | x | x | x | x | x | | x | | x | | x | x | | | x |
| *Globigerinoides sacculifer* | x | x | x | x | x | x | x | x | x | x | x | | | x | | | x | | x | |
| *Globigerinoides seigliei* | | | | | | | | | | | | | | | | | | | | |
| *Globorotalia crassaformis* | | | | | | | | | | | | x | | x | | | x | | | |
| *Globorotalia exilis* | | | | | | | | | | | | | | | | | | | | |
| *Globorotalia juanai* | | | | | | | | | | | | | | | | | | | | |
| *Globorotalia margaritae* | | | | | | | | | | | | | | | | | | | | |
| *Globorotalia menardii* | | | | | | | | x | | x | | x | x | x | | | | | | |
| *Globorotalia miocenica* | | | | | | | | | | | | | | | | | | | | |
| *Globorotalia plesiotumida* | | | | | | | | | | | | | | | | | | | | |
| *Globorotalia pseudomiocenica* | | | | | | | | | | | | | | | | | | | | |
| *Globorotalia puncticulata* | | | | | | | | | | | | | | | | | | | | |
| *Globorotalia scitula* | | | | | | | | | | | | | | | | | | | | |
| *Globorotalia tosaensis* | | | | | | | | | | | | | | | | | | | | |
| *Globorotalia truncatulinoides* | | x | x | x | | | x | | x | | | | | | | | | x | | |
| *Globorotalia tumida* | | x | | | | | | | | | | | | x | | | | | | |
| *Neogloboquadrina acostaensis* | | | x | x | x | | | | | | | | | | | | x | | | |
| *Neogloboquadrina dutertrei* | x | x | x | x | | x | x | x | | x | x | | x | x | | | x | | | |
| *Neogloboquadrina humerosa* | | x | x | x | x | x | x | | | x | | | | x | | | | | | |
| *Neogloboquadrina pachyderma* | | | | | | | | | | x | | | | | | | | | | |
| *Orbulina universa* | x | x | x | x | x | x | | x | | x | | | x | x | | | x | | | |
| *Pulleniatina obliquiloculata* | x | | x | x | | | | | x | | x | x | x | x | | x | | x | | |
| *Pulleniatina primalis* | | | | | | | | | | | | | | | x | | x | | | |
| *Sphaeroidinella dehiscens* | | | x | | x | | | | x | x | x | | x | x | x | x | x | | | |
| *Sphaeroidinellopsis* sp. | | | | | | | | | ? | | | | | ? | | | | | | |
| *Turborotalia quinqueloba* | | | | | | | | | | | | | | | | | | | | |

He assigned the overlying post-Uscari fossiliferous beds to the Gatun Formation. For a detailed lithostratigraphy of the Limon Group see Coates *et al.* (1992) and Coates (Chapter 1, this volume).

### *Uscari Formation*

Previous foraminiferal studies of the Uscari Formation include Goudkoff and Porter (1942), Taylor (1975), Cassell (1986), Pizarro (1987), and Cassell and Sen Gupta (1989a). The following species of planktic foraminifera were identified in this formation in a study by Pizarro (1987): *Globorotalia siakensis* ( = *Globorotalia mayeri* in Bolli and Saunders, 1982; LAD = 10.2 Ma), *Globigerina nepenthes* (LAD = 4.0 Ma), *Sphaeroidinellopsis seminulina* and *S. paenedehiscens* (LAD = 3.0 Ma), *Dentogloboquadrina altispira* (LAD = 2.9 Ma), *Globigerina venezuelana* (LAD = 3.4 Ma) and *Globigerinoides extremus* (FAD = 7.2 Ma). Bolli and Saunders (1985) considered *S. paenedehiscens* to be a synonym of *S. seminulina*, which they gave a FAD of 7.2 Ma. Therefore, Pizarro's extension of the Uscari Formation into the Late Miocene is confirmed by the presence of *S. seminulina* and *G. extremus*.

Pizarro (1987) also identified *Catapsydrax dissimilis* and *C.* cf. *C. unicavus,* which he believes were reworked and therefore not representative of the sediments in which they were found. Upon viewing the scanning electron micrographs of these specimens, they appear to be *Dentogloboquadrina venezuelana*

Table 2.—Continued.

| | Shark Hole Point Fm. | | | | | | Nancy Point Fm. | | | | | | | Cayo Agua Fm. | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 379- | 376- | 384- | 389- | 388- | 390- | 393- | 396- | 397- | 401- | 407- | 410- | 411 | 338- | 337- | 336- | 335- | 334- | 300- | 298- | 293- |
| *Candeina nitida* | | | | | | | | | | | | | | | | | x | | | | |
| *Dentoglobоquadrina altispira* | x | x | x | x | x | | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x |
| *Globigerina apertura* | | x | x | | x | | | x | x | x | x | x | | | x | | x | | x | x | x |
| *Globigerina bulloides* | x | x | x | x | x | | x | x | x | x | x | | x | | x | | x | | x | x | x |
| *Globigerina decoraperta* | | x | x | x | x | x | x | x | x | x | x | x | | | | | x | x | x | x | |
| *Globigerina falconensis* | | | | x | x | | x | x | x | x | x | | | | x | | | | x | x | x |
| *Globigerina nepenthes* | | x | x | x | x | | | | | x | x | x | | | | | | | | | |
| *Globigerina woodi* | | | x | x | | | x | x | | | | x | x | | | | | x | | | |
| *Globigerinella aequilateralis* | | x | x | x | | | x | x | | x | x | x | | | x | | x | x | x | x | x |
| *Globigerinella calida* | | | | | | | | | | | | | | | | | | | | | |
| *Globigerinita glutinata* | x | x | x | x | | | | x | x | x | x | x | | | | | | x | | | x |
| *Globigerinoides conglobatus* | | | x | | | | x | | | x | | | | | | | x | x | | | |
| *Globigerinoides obliquus* | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x |
| *Globigerinoides ruber* | | x | x | | | | x | x | x | x | | x | | | x | x | x | x | x | x | x |
| *Globigerinoides sacculifer* | x | x | x | x | x | x | x | | x | x | x | x | | | x | | x | x | x | x | x |
| *Globigerinoides seigliei* | | | | | | | x | | | x | | | | | | | | | | | |
| *Globorotalia crassaformis* | | | | | | | | | | | | | | | | | | | | | |
| *Globorotalia exilis* | | | | | | | | | | | | x | | | | | | | | | |
| *Globorotalia juanai* | | | | | | | | | x | | | x | x | | | | | | | | |
| *Globorotalia margaritae* | | x | x | | | | | | | | | | | | | | | | | | |
| *Globorotalia menardii* | x | | | | x | x | x | x | x | | x | x | | | | | | | | | x |
| *Globorotalia miocenica* | | | | | | | | | | | | | | | | | | | | | |
| *Globorotalia plesiotumida* | x | x | x | x | x | x | | | | x | x | x | x | x | x | x | x | x | x | x | |
| *Globorotalia pseudomiocenica* | | | | | | | x | | | | | | | | | | | | | | |
| *Globorotalia puncticulata* | | | | | | | | | | | | | | | | | | | | | |
| *Globorotalia scitula* | | | | | | | | | | | x | x | | | | | | | | | |
| *Globorotalia tosaensis* | | | | | | | | | | | | | | | | | | | | | |
| *Globorotalia truncatulinoides* | | | | | | | | | | | | | | | | | | | | | |
| *Globorotalia tumida* | | | | | | | | x | x | | | | | | | | | | | | |
| *Neogloboquadrina acostaensis* | x | x | x | x | x | x | x | x | | x | x | x | x | | | | | | x | | |
| *Neogloboquadrina dutertrei* | | | | | | | | | | | | | | | | | | | | | |
| *Neogloboquadrina humerosa* | | | | | x | x | x | x | x | x | | | | | x | | x | x | | x | x |
| *Neogloboquadrina pachyderma* | | x | x | | | | x | | | x | x | x | | | | | | x | | | |
| *Orbulina universa* | | x | x | | | x | x | x | x | x | x | x | x | | | | | x | | x | x |
| *Pulleniatina obliquiloculata* | | | | | | | | | | | | | | | | | | | | | |
| *Pulleniatina primalis* | x | x | | | | | | | | x | | | | | | | | | | | |
| *Sphaeroidinella dehiscens* | | | | | | | | | | | | | | | | | | | | | |
| *Sphaeroidinellopsis* sp. | | x | x | x | x | | x | x | x | | | | | | | | x | | | | |
| *Turborotalia quinqueloba* | | | | | | | | | | | | | | | | | | | | | |

with an aberrant last chamber which sometimes forms in this species and leads to confusion in identification (Bolli and Saunders, 1985; p. 186). The specimens which Pizarro labelled as *Catapsydrax dissimilis* and *C.* cf. *C. unicavus* appear to have an aberrant last chamber with similar wall texture to the chambers of the test. True bullae usually exhibit a wall texture which differs from that of the chambers.

Cassell and Sen Gupta (1989a) sampled three separate sections from three different river valleys and analyzed the foraminifera. Based on their planktic foraminiferal identifications, they concluded that the Uscari Formation spans Zones N3 to N10 (or Upper Oligocene to Middle Miocene). The Uscari Formation may possibly include sediments younger than Zone N10, but they did not have access to the upper portion of the type section along Quebrada Uscari. *Globorotalia kugleri* was found at the base of the formation and is diagnostic of the earliest Miocene (approximately 23.7–21.8 Ma; Zhang *et al.*, 1993). The FAD of this species marks the Oligocene–Miocene boundary in the newly proposed Oligocene–Miocene boundary stratotype (Steinenger *et al.*, 1996). Less than 10 m above the base occur *Catapsydrax stainforthi, C. dissimilis* and *Globorotalia fohsi peripheroronda,* all indicative of the Early Miocene.

In this study only the uppermost Uscari Formation was sampled. The four samples analyzed (PPP 726, 735–737; Table 2) appear to be approximately coeval with the lower portion of the Nancy Point Formation

Table 2.—Extended.

| | Cayo Agua Fm. | | | | | | | Escudo de Veraguas Fm. | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | -61 | 374 | 373 | 372 | 371 | 307 | 306 | 168 | 169 | 170 | 358 | 360 | 361 | 362 | 364 | 365 | 366 | 367 | 368 | 369 |
| *Candeina nitida* | | | | x | | | | | | | | | | | | | | | | |
| *Dentogloboquadrina altispira* | x | x | x | x | x | x | x | | x | | | | | | | | | | | |
| *Globigerina apertura* | x | x | x | x | | x | | x | x | | | x | x | x | x | | | | | x |
| *Globigerina bulloides* | x | x | x | x | x | x | | x | x | | | x | | x | | | | | | x |
| *Globigerina decoraperta* | | x | x | x | x | x | | | x | | | | x | x | | x | | | | x |
| *Globigerina falconensis* | x | x | x | x | x | x | | x | x | | x | x | x | x | | | x | x | | |
| *Globigerina nepenthes* | | x | | | | | | | | | | | | | | | | | | |
| *Globigerina woodi* | x | x | | | | | | | | | | x | x | | | x | x | | | |
| *Globigerinella aequilateralis* | x | x | x | x | | x | | x | x | x | | | x | x | | x | x | x | x | x |
| *Globigerinella calida* | | | | | | | | x | | | | | | | | | | | | |
| *Globigerinita glutinata* | | x | | x | x | | | x | x | | | x | x | x | x | x | | | | x |
| *Globigerinoides conglobatus* | | | | | | x | | | | | | | | x | | | | | | x |
| *Globigerinoides obliquus* | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x |
| *Globigerinoides ruber* | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x |
| *Globigerinoides sacculifer* | x | x | x | x | x | x | x | x | x | | x | x | x | x | x | x | | x | x | x |
| *Globigerinoides seigliei* | | | | | | | | | | | | | | | | | | | | |
| *Globorotalia crassaformis* | | | | | | | | x | x | x | | x | x | x | | | | | x | |
| *Globorotalia exilis* | | x | | | | | | | | | | x | | | | | | | | |
| *Globorotalia juanai* | | | | | | | | | | | | | | | | | | | | |
| *Globorotalia margaritae* | x | x | | x | | | | | | | | | | | | | | | | |
| *Globorotalia menardii* | x | x | x | x | | | x | | | | | | | | | | | | | |
| *Globorotalia miocenica* | | | | | | | | | | | | x | x | x | x | x | x | x | | x |
| *Globorotalia plesiotumida* | x | x | | x | | x | | | | | x | | | | | | | | | |
| *Globorotalia pseudomiocenica* | | | | | | | | | | | | | x | x | x | | | | x | |
| *Globorotalia puncticulata* | x | | | | | | | | | | | | | | | | | | | |
| *Globorotalia scitula* | | | | | | | | | | | | x | | | | | | | | |
| *Globorotalia tosaensis* | | | | | | | | | | | | | | x | | | | | | |
| *Globorotalia truncatulinoides* | | | | | | | | | | | | x | | | | | | | | |
| *Globorotalia tumida* | | | | | | | | | | | | | | | | | | | | |
| *Neogloboquadrina acostaensis* | x | x | | x | x | | | x | x | | x | x | x | x | | | | | | x |
| *Neogloboquadrina dutertrei* | | | | | | | | x | | x | | | | | x | | | | | |
| *Neogloboquadrina humerosa* | x | x | x | x | | x | | x | x | | | x | x | x | | | | | | x |
| *Neogloboquadrina pachyderma* | | | | x | | | | x | x | | | | | | | | | | | |
| *Orbulina universa* | x | | x | x | x | x | x | x | x | | x | x | x | x | x | | x | x | | x |
| *Pulleniatina obliquiloculata* | | | | | | | | x | x | | | | | | | | | | | |
| *Pulleniatina primalis* | | x | | | | | | | | | | | | | | | | | | |
| *Sphaeroidinella dehiscens* | | | | | | | | | | | | | | x | | | | | | |
| *Sphaeroidinellopsis* sp. | x | x | x | | | | | | | | | | | | | | | | | |
| *Turborotalia quinqueloba* | | | | | | | | x | | | | | x | x | | x | | x | | |

(Late Miocene) of Panama and therefore are the youngest dated samples collected from the Uscari Formation. These samples were collected from two locales (Appendix A, Map 10): (1) Carbon Dos Road, south of Limon and west of Punta Cahuita, and (2) Rio Sandbox, south of Limon and southwest of Punta Cahuita. Planktic foraminifera identified from one sample, PPP 726, of the Carbon Dos section (Section 28, Appendix B) include *Globorotalia juanai* (FAD = 10.4, LAD = 7.2 Ma) and left-coiled *G. menardii* and *Globorotalia plesiotumida* (FAD = 7.7; LAD = 4.0 Ma). Planktic foraminifera identified from the Rio Sandbox section (PPP 735–737, Section 27, Appendix B) include *Globigerina nepenthes* (LAD = 4.0 Ma) and *Globorotalia plesiotumida,* which undergoes an abrupt coiling change from sinistral to dextral between the middle and uppermost samples (PPP 735, 737) in the section. The total species diversity ranged from 6 to 13 per sample with a mean of 10 for the Uscari Formation, which is the highest for the Limon Group. The nannofossil results place 2 of 3 samples from Carbon Dos and both Rio Sandbox samples in Zone NN 11 (approximate age = 8.2–5.6 Ma) based on the occurrences of *Discoaster berggrenii* and/or *D. quinqueramus.*

In summary, Pizarro (1987) apparently had samples of the Uscari Formation ranging in age from Middle to Late Miocene. Cassell and Sen Gupta (1989a) sampled the base of the formation, which has a maximum age of Early Miocene based on the occurrence of *Glo-*

Table 3.—Neogene events of planktic foraminifera (F) and calcareous nannoplankton (N) used in this study (modified from Coates *et al.*, 1992). Datums with an asterisk are held with lower confidence. Reapp. = reappearance, disapp. = disappearance, FAD = first appearance datum, LAD = last appearance datum.

| Type | Taxon | Event | Age (Ma) | Notes |
|---|---|---|---|---|
| N | *Pseudoemiliania lacunosa* | LAD | 0.5 | |
| N | *Calcidiscus macintyrei* | LAD | 1.5 | |
| N | *Gephyrocapsa* spp. (large) | FAD | 1.7 | |
| F | *Globigerinoides obliquus/extremus* | LAD | 1.8 | |
| F | *Globorotalia truncatulinoides* | FAD | 1.9 | |
| N | *Discoaster brouweri* | LAD | 1.9 | |
| F | *Globorotalia miocenica* | LAD | 2.2 | Atlantic only |
| F | *Globorotalia menardii*, left-coiled | FAD | 2.2 | coiling event |
| F | *Globorotalia menardii*, right-coiled | LAD | 2.2 | coiling event |
| F | *Pulleniatina* spp. | reapp. | 2.2 | Atlantic only |
| N | *Discoaster pentaradiatus* | LAD | 2.4 | |
| N | *Gephyrocapsa* spp. (small) | FAD | 2.5* | |
| F | *Dentoglobоquadrina altispira* | LAD | 2.9 | |
| F | *Sphaeroidinella dehiscens* | FAD | 3.0 | |
| F | *Sphaeroidinellopsis* spp. | LAD | 3.0 | |
| F | *Globorotalia tosaensis* | FAD | 3.1 | |
| F | *Pulleniatina* spp. | disapp. | 3.3 | Atlantic only |
| F | *Globorotalia miocenica* | FAD | 3.4 | Atlantic only |
| F | *Globorotalia margaritae* | LAD | 3.4 | |
| F | *Globigerinoides ruber* | reapp. | 3.5* | |
| N | *Sphenolithus abies* | LAD | 3.5 | |
| N | *Reticulofenestra pseudoumbilicus* | LAD | 3.5 | |
| N | *Pseudoemiliania lacunosa* | FAD | 3.6 | |
| F | *Pulleniatina*, right-coiled | FAD | 3.7 | coiling event |
| F | *Pulleniatina*, left-coiled | LAD | 3.7 | coiling event |
| F | *Globorotalia puncticulata* | FAD | 4.0 | |
| F | *Globorotalia plesiotumida* | LAD | 4.0* | |
| F | *Globigerina nepenthes* | LAD | 4.0 | |
| F | *Globorotalia crassaformis* | FAD | 4.3 | |
| F | *Globigerinoides seigliei* | LAD | 4.3 | |
| N | *Ceratolithus acutus* | LAD | 4.6 | |
| N | *Ceratolithus acutus* | FAD | 5.0 | |
| F | *Globorotalia tumida* | FAD | 5.2* | |
| F | *Globigerinoides conglobatus* | FAD | 5.3 | |
| F | *Globorotalia margaritae* | FAD | 5.6 | |
| N | *Discoaster quinqueramus* | LAD | 5.6 | |
| N | *Discoaster berggrenii* | LAD | 5.6 | |
| F | *Globorotalia plesiotumida* | FAD | 6.3 or 7.7* | |
| F | *Globorotalia juanai* | LAD | 7.2 | |
| F | *Neogloboquadrina humerosa* | FAD | 7.5 | |
| N | *Discoaster quinqueramus* | FAD | 8.2 | |
| F | *Globorotalia juanai* | FAD | 10.4 | |
| F | *Globigerina nepenthes* | FAD | 11.3 | |

*borotalia kugleri.* The stratigraphically highest samples they dated belong to Zone N10 (estimated age = 14.8 to 13.9 Ma) or Middle Miocene based on the cooccurrence of *Globorotalia fohsi peripheroronda* and *Orbulina universa.* The limited samples from the uppermost Uscari Formation used in this study indicate a Late Miocene age with the combined planktic foraminiferal-nannofossil estimate ranging from 7.7 to 5.6 Ma for the Rio Sandbox section, and 7.7 to 7.2 Ma for the Carbon Dos section.

### *Rio Banano Formation*

The Rio Banano Formation was named by Taylor (1975), who assigned the strata to Zones N17–N21 (Upper Miocene to Upper Pliocene). Cassell (1986) and Cassell and Sen Gupta (1989b) restricted the middle portion of the Rio Banano to Lower Pliocene (lower Zone N18, ~5.3 Ma) using the stratigraphic overlap of planktic foraminifera, particularly *G. extremus* and *G. ruber,* and an ostracode species, *Radimella ovata.* Since both the upper and lower portions of the Rio

Banano Formation produced no age-diagnostic foraminiferal species, they extrapolated the age of the Rio Banano Formation from the Late Miocene to the Late Pliocene.

Sixteen samples of Rio Banano deposits used in this study were collected from two localities in southeastern Costa Rica. Map 11 and Inset C of Map 11, Appendix A, show the localities, and Sections 29 and 32, Appendix B, show the stratigraphic order of samples in each of the sections. Fourteen samples (PPP 668, 670, 672, 678, 679, 682–690; Table 2) were collected from the type section (Section 29, Appendix B) along the Banano River, west of Bomba. Two samples (PPP 720 and 721) were collected from the Santa Rita locality (Map 11, Appendix A; Section 32, Appendix B), south of Moin. In general, the planktic foraminifera were sparse, poorly preserved, and of low diversity (total species diversity ranged from 2 to 12 per sample with a mean of 7) in this formation.

Species found in the Bomba section (Inset C of Map 11, Appendix A; Section 29, Appendix B) include *Dentoglobigerina altispira* (LAD = 2.9 Ma), *Globigerinoides ruber*, *G. sacculifer, G. obliquus,* and right-coiled *Globorotalia plesiotumida* (FAD = 7.7 Ma; LAD = 4.0 Ma). *Dentoglobigerina altispira* has a last occurrence in the upper fifth of the section. *Globigerinoides ruber* and *G. obliquus* occur in equal numbers (% ruber ≈ 0.5). The top of the section lacks *D. altispira,* but contains *G. conglobatus* (FAD = 5.3 Ma) and *Globorotalia plesiotumida,* which has a LAD in the Early Pliocene in mid-Zone N19 (or approximately 4.0 Ma based on Kennett and Srinivasan, 1983, and Bolli and Saunders, 1985. Neogloboquadrinids occur throughout the section with *Neogloboquadrina dutertrei* occurring in the top of the section and *Neogloboquadrina acostaensis* scattered throughout the section.

Nannofossils were also rare or lacking in many of the samples processed from this formation. However, key taxa that were identified include *Sphenolithus abies* (LAD = 3.5 Ma) and *Pseudoemiliania lacunosa* (3.6–0.5 Ma) occurring together from the base through nine tenths of the section, where *S. abies* last occurs (at PPP 676). Uppermost samples contain small *Gephyrocapsa* sp. (FAD = 2.5) in association with *Discoaster pentaradiatus* (LAD = 2.4 Ma).

The Santa Rita section (at PPP 720 and 721; Section 32, Appendix B) contains an equivalent planktic fauna to the Bomba section. Planktic foraminifera include *Dentoglobigerina altispira, Globigerinoides conglobatus, Globorotalia plesiotumida* and right-coiled *G. menardii.* Calcareous nannofossils include *P. lacunosa, D. pentaradiatus* and a few isolated occurrences of small *Gephyrocapsa* spp.

In summary, planktic foraminifera of the Rio Banano Formation offer weak age information primarily relying on the presence of *G. plesiotumida.* This species puts the base of the formation (at PPP 679) between 7.7 and 4.0 Ma. The top (at PPP 668) has a maximum age of 5.3 Ma based on the presence of *Globigerinoides conglobatus.* However, negative evidence suggests the top to be ≤ 2.9 Ma based on the absence of *Dentoglobigerina altispira,* which last occurs near the top of the formation (at PPP 690). The presence of *G. ruber* suggests an age of ≤ 3.5 Ma (Table 2). The presence of *Globorotalia plesiotumida* at the top of the formation offers conflicting evidence as it has a LAD of 4.0 Ma. However, in ranking the confidence of identifications, *G. plesiotumida* would rank low because of its similarity to other *menardii*-form globorotaliids. On the other hand, nannofossil data suggest a younger base at 3.6 to 3.5 Ma, while they suggest a more refined younger age for the top at 2.5 to 2.4 Ma. The conflict between the nannofossil- and the foraminifera-based age estimates lies in the identification and geologic range of *G. plesiotumida.* Since this author has less confidence in the identification and the geologic range for this species, the nannofossil-based age estimates are considered more reliable for this formation. However, it is interesting to note that Cassell and Sen Gupta (1989b) showed the Rio Banano extending to the base of the Pliocene, which supports the older foraminiferal-based date from this study.

### *Moin Formation*

Akers (1972) provided the first age determination for the Moin Formation (Early Pleistocene) using planktic foraminifera based on one locality—TU 954 of Vokes, a hill cut behind the Standard Fruit Company, west of the Pueblo Nuevo Cemetery, approximately 2 km west of Limon. His key taxa were *Neogloboquadrina dutertrei, Sphaeroidinella dehiscens, Globigerinoides obliquus, Globigerinoides conglobatus* and *Pulleniatina obliquiloculata.* Using the LADs and FADs of this association gives an age span of 3.0–1.8 Ma or Late Pliocene. *Globigerinoides obliquus* became extinct 1.8 Ma and *S. dehiscens* evolved 3.0 Ma. *Neogloboquadrina dutertrei* evolved in the Pliocene and does not necessarily indicate a Pleistocene age (Bolli and Saunders, 1985, p. 211). If one uses the Atlantic reoccurrence date of *Pulleniatina* at 2.2 Ma (Saito, 1976; Keigwin, 1982) it would narrow the age restriction to 2.2–1.8 Ma. The Atlantic reoccurrence date of *Pulleniatina* refers to its disappearance from the Atlantic depositional record at 3.3 Ma and reappearance at 2.2 Ma, while its Pacific fossil record is continuous through this period.

Cassell (1986) dated the Moin Formation as Pleistocene based on the occurrence of *Globorotalia truncatulinoides excelsa* (FAD = 1.9 Ma) and *Sphaeroidinella dehiscens-excavata,* which Cassell considered to be restricted to the Pleistocene. However, Bolli and Saunders (1985) and Dowsett (oral commun., 1991) stated that this form (*Sphaeroidinella dehiscens-excavata*) originated in the Pliocene.

Planktic foraminifera identified in this study came from twenty samples (Table 2) taken from six Costa Rica locales: 1) near Pueblo Nuevo Cemetery, 1 km west of Limon (PPP 631, Section 35, Appendix B; 635–637, Section 36, Appendix B); 2) Lomas del Mar, west of Limon (PPP 638, 643, 645; Section 36, Appendix B); 3) an unnamed creek near Cangrejos (to be called "Cangrejos Creek" herein), west of Limon (PPP 647, 648, 650, 652–658, Section 37, Appendix B); 4) west of Rio Blanco, south of Limon (PPP 705, no drawn section); 5) southwest of Liverpool (PPP 710, in Section 36, Appendix B); 6) Route 32, west of Pueblo Nuevo Cemetery (PPP 712, in Section 34, Appendix B). All PPP numbers are shown in Appendix A on Inset B of Map 11 except PPP 705, which is shown on Map 11.

Planktic foraminifera identified from near Pueblo Nuevo Cemetery (Section 36, Appendix B) include left-coiled *Globorotalia truncatulinoides* (FAD = 1.9 Ma), *Sphaeroidinella dehiscens* (FAD = 3.0 Ma), *Globigerinoides conglobatus* (FAD = 5.3 Ma), and right-coiled *Pulleniatina obliquiloculata,* which reappeared in the Caribbean at 2.2 Ma. Since *Globorotalia truncatulinoides* occurs near the base, the entire section is probably <1.9 Ma. The total species diversity of planktic foraminifera for the Moin Formation ranges from 2 to 15 per sample with a mean of 7, equal to the underlying Rio Banano despite the greater abundance and better preservation.

At Lomas del Mar, *G. truncatulinoides* (FAD = 1.9 Ma) was found throughout this part of the section (middle of Section 36, Appendix B), confirming the age to be < 1.9 Ma. Also noted was a coiling change from right to left between samples PPP 643 and 638. However, due to the complex coiling history of *G. truncatulinoides* in the Caribbean, correlating such an event does not carry much confidence.

The Cangrejos Creek locale (Section 37, Appendix B) produced abundant and diverse, well-preserved planktic foraminifera. Key taxa found consistently throughout the section are right-coiled *Pulleniatina (P. obliquiloculata* and *P. primalis*) and *Sphaeroidinella dehiscens* (FAD = 3.0 Ma). *Globorotalia truncatulinoides* (FAD = 1.9 Ma) was also identified throughout this section. *Globigerinoides obliquus* (LAD = 1.8 Ma) was found in one sample (PPP 658) with *G. truncatulinoides,* restricting the age of that sample to 1.9–1.8 Ma. Two specimens of sphaeroidinellids lacking secondary apertures as in *Sphaeroidinellopsis* sp. (LAD = 3.0 Ma) were identified in two samples (PPP 655, 658). These specimens are small relative to the larger, co-occurring *Sphaeroidinella dehiscens,* and are considered by the author to be juvenile forms of *S. dehiscens.* Bolli and Saunders (1985) discussed *Sphaeroidinella* and *Sphaeroidinellopsis* in detail and stated that juvenile forms of the former do not always exhibit the secondary aperture(s) which define the genus *Sphaeroidinella,* and appear to be the ancestral *Sphaeroidinellopsis*, (also refer to Berggren, 1993, for discussion on *Sphaeroidinella* and *Sphaeroidinellopsis*). The remaining three locales of the Moin Formation did not produce any age-indicative planktic foraminiferal taxa.

In summary, planktic foraminifera indicate that the Moin Formation is restricted to 1.9 Ma and younger based on the occurrence of *G. truncatulinoides* (FAD = 1.9 Ma). The consistent occurrence of right-coiled *Pulleniatina obliquiloculata,* suggesting an age no greater than 2.2 Ma (Saito, 1976; Keigwin, 1982), supports this. Left-coiled *Globorotalia menardii* also suggests an age of 2.2 Ma or younger (Bolli and Saunders, 1985).

Coates *et al.* (1992) date the base of the Moin at 3.0 Ma based on the co-occurrence of *Sphaeroidinella* and *Sphaeroidinellopsis*; however, the author believes the *Sphaeroidinellopsis*-like specimens lacking secondary apertures may be an example of ontogeny recapitulating phylogeny (Gould, 1977). Further investigation, including ontogenetic studies of living *Sphaeroidinella* sp., is necessary to determine what characters are useful in distinguishing members in this genus from members of the ancestral genus, *Sphaeroidinellopsis.*

Nannofossils were identified from 27 Moin Formation samples taken from the Pueblo Nuevo Cemetery (4 samples), Lomas del Mar (6 samples), and Cangrejos Creek (11 samples) locations. Key nannofossils identified from the Pueblo Nuevo (lower) part of the Lomas del Mar Eastern Sequence (Section 36, App. B) include *Sphenolithus abies* (LAD = 3.5 Ma), *Pseudoemiliania lacunosa* (3.6–0.5 Ma), *Calcidiscus macintyrei* (LAD = 1.5 Ma), *Discoaster pentaradiatus* (LAD = 2.4 Ma), *D. brouweri* (LAD = 1.9 Ma), and *D. berggrenii* (LAD = 5.6 Ma). Additional older nannofossils were found which are clearly reworked. In fact, *D. berggrenii* and some of the *S. abies* are apparently reworked as the planktic foraminiferal faunas discussed above are clearly younger than these two nannofossil species would indicate. Based on the species consistently occurring in these samples, the lower section (12–24 m) is >1.9 Ma and <3.6 Ma.

Stratigraphically above this, at Lomas del Mar (Section 36, App. B, 30–38 m), *Pseudoemiliania lacunosa* (3.6–0.5 Ma) occurs throughout this part of the section with *Discoaster brouweri* (LAD = 1.9 Ma), placing this part also at 3.6–1.9 Ma. The specimens of *S. abies* (LAD = 3.5 Ma) at the top of this part (at PPP 640) are probably reworked, based on the presence of *Globorotalia truncatulinoides* (FAD = 1.9 Ma) in a sample (PPP 638) 1.5 m below.

At Cangrejos Creek (Section 37, App. B), nannofossils were identified in eleven samples. The species occurring most frequently throughout the section are large *Gephyrocapsa* (FAD = 1.7 Ma), *P. lacunosa* (3.6–0.5 Ma) and *C. macintyrei* (LAD = 1.5 Ma), thus placing the entire section between 1.7 and 1.5 Ma. These dates concur with those based on the planktic foraminifera. Older nannofossils, including *D. berggrenii* and *S. abies,* were identified in one sample (PPP 647) but are most likely reworked, based on the younger fauna found in the same sample.

Integrated nannofossil and planktic foraminifera data suggest that the top of the Moin Formation is restricted to 1.7–1.5 Ma (nannofossils) and the base is as old as 1.9 Ma based on the combined evidence of *D. brouweri* (LAD = 1.9 Ma) and *G. truncatulinoides* (FAD = 1.9 Ma).

## BOCAS DEL TORO GROUP

The sediments that comprise this group in northwestern Panama were only recently described in detail by Coates *et al.* (1992) for the Panama Paleontology Project. Prior to that study, the only published references were brief mentions by Terry (1956) and Olsson (1922, 1942). In general, these sediments consist of approximately 600 meters of re-worked, nearshore volcaniclastic sediments that were deposited in a backarc setting in the Bocas del Toro Basin. The calcareous microfossils found in these units are abundant and well-preserved, and indicate an approximate age range of Late Miocene to Early Pleistocene.

### *Nancy Point Formation*

The Nancy Point Formation is composed of approximately 500 m of sediments which are Late Miocene in age. These sediments crop out along the northeastern coast of Valiente Peninsula from the western margin of Shark Hole Point to Nancy Point (Map 5, Appendix A).

Planktic foraminifera were identified from seven samples (PPP 393, 396, 397, 401, 407, 410, 411; Table 2) of the Nancy Point Formation. Their locations are shown on Insets D–F of Map 5, Appendix A, and relative stratigraphic positions are plotted on Section 12, Appendix B. Key taxa identified near the base of the formation (at PPP 410–411) include *Dentoglobigerina altispira* (LAD = 2.9 Ma), *Globigerina nepenthes* (LAD = 4.0 Ma) and *Globorotalia juanai* (10.4–7.2 Ma). Coates *et al.* (1992) used the FAD of *Globorotalia exilis* found (one specimen) at PPP 410 to place a maximum date of 6.5 Ma. However, Kennett and Srinivasan (1983) placed the FAD of *G. exilis* in mid-N18, which they equated with Late Miocene, while Bolli and Saunders (1985) placed the FAD in the Early Pliocene Zone N18 (Berggren *et al.*, 1985). The uncertainty of the FAD and the possibility that the specimen was a contaminant suggest that *G. exilis* is a less reliable age indicator. Planktic foraminifera that were identified near the top of the Nancy Point Formation (PPP 393) include *Globigerinoides conglobatus, Dentoglobigerina altispira, Sphaeroidinellopsis* sp. and *G. seigliei* (LAD = 4.3 Ma) to give an age range of 5.3–4.3 Ma for the top of Nancy Point Formation. The total species diversity (planktic foraminifera) of the Nancy Point Formation ranged from 10 to 19 per sample with a mean of 16, the highest among the formations examined in this study.

Nannofossils from near the base and top of the Nancy Point Formation include *Discoaster quinqueramus* and *D. berggrenii* (both with a FAD of 8.2 Ma and a LAD of 5.6 Ma), which restrict the formation to NN 11 or 8.2–5.6 Ma. In summary, the Nancy Point Formation is constrained to 5.6–5.3 Ma (*Globigerinoides conglobatus* and *D. berggrenii*) at the top and 8.2–7.2 Ma (*Globorotalia juanai* and *D. quinqueramus*) at the base.

### *Shark Hole Point Formation*

Overlying the Nancy Point Formation is the ~340-m-thick Shark Hole Point Formation, which is Early Pliocene in age. The Shark Hole Point Formation crops out east of the Nancy Point Formation along the coast of the Valiente Peninsula from Bruno Bluff to the eastern margin of Shark Hole Point (Map 5 and Inset F, Appendix A). Planktic foraminifera were identified from five samples (PPP 376, 379, 384, 388–390; Table 2) of the Shark Hole Point Formation. Their relative stratigraphic positions are plotted on Section 12, Appendix B. *Globigerinoides* spp. are abundant, while *Globorotalia plesiotumida* (right-coiled), *Globigerina bulloides* and *G. falconensis* consistently occur throughout the formation. *Neogloboquadrina* spp. occur in low abundance. The total species diversity for the Shark Hole Point Formation ranged from 8 to 18 per sample with a mean of 13, less than the underlying Nancy Point Formation but greater than the other formations in this study.

The key planktic foraminifera identified from the base of the Shark Hole Point Formation (at PPP 388) are *Dentoglobigerina altispira* (LAD = 2.9 Ma), *Sphaeroidinellopsis noitals* (LAD = 3.0 Ma) and *Globigerina nepenthes* (LAD = 4.0 Ma). The latter form occurs through this formation, which suggests a pre-4.0-Ma age for most of the formation. *Dentoglobigerina altispira, Globorotalia plesiotumida* (right-coiled) *Sphaeroidinellopsis* sp., *Pulleniatina primalis* (left-coiled) and *Globorotalia margaritae* (at PPP 376) are present near the top of the section. *Globorotalia margaritae* restricts the maximum date to 5.6 Ma (Table 2); however, the presence of *Globigerinoides conglobatus* in a lower sample, midway in the section (at PPP 384), restricts the age of the overlying samples to a post-5.3-Ma age. *Pulleniatina primalis* undergoes a coiling change from left to right at ~ 3.7 Ma. Therefore, the minimum age would be 3.7 Ma. Due to the lower confidence in *G. plesiotumida*, it is not used here.

The nannofossils *Sphenolithus abies* (LAD = 3.5 Ma) and *Reticulofenestra pseudoumbilicus* (LAD = 3.5 Ma) occur consistently in the Shark Hole Point Formation, which suggests a minimum age of 3.5 Ma. The uppermost sample is barren of calcareous nannofossils; however, *Pseudoemiliania lacunosa* (3.6–0.5 Ma) occurs in the top quarter of the section at PPP 376, which limits the maximum age of the top of the formation to 3.6–3.5 Ma. No maximum age for the base is suggested by the calcareous nannofossils.

In summary, the combined data provide an age range of 5.3 to 3.7 Ma or Early Pliocene for the Shark Hole Point Formation. In a study by Dowsett and Cotton (1996) in which graphic correlation analysis was applied to both the nannofossil and planktic foraminifera data, the age estimates for the Shark Hole Point Formation were 5.68 to 3.28 Ma (note: samples now considered the top of Nancy Point Formation were originally considered the base of the Shark Hole Point Formation when the graphic correlation was applied. Thus, the maximum date of 5.68 Ma would represent an age for the top of Nancy Point Formation and the base of Shark Hole Point Formation would be younger than 5.68 Ma by necessity).

### *Cayo Agua Formation*

Sediments of the Cayo Agua Formation crop out along the northeastern coast of the island of Cayo Agua which lies along the northern limit of the Chiriqui Lagoon, west of the Valiente Peninsula (Map 6 and Insets, Appendix A). These sediments are approximately Early to middle Pliocene in age. Planktic foraminifera were identified from fifteen samples of the Cayo Agua Formation (PPP 371–374, 61, 306, 307, 293, 298, 300, 334–338; Table 2). Their relative stratigraphic positions are plotted on Sections 19–20, Appendix B.

The faunas in this formation typically have few *Neogloboquadrina* spp. and abundant *Globigerinoides* spp. with *G. obliquus* consistently dominant relative to *G. ruber. Dentoglobigerina altispira* occurs consistently throughout the section and in greater relative abundance than in any other formation in this study. *Globigerina bulloides* and *G. falconensis* are subdominant in parts of the section. The total species diversity for the Cayo Agua Formation ranged from 3 to 20 per sample with a mean of 12, lower than the Nancy Point and Shark Hole Point formations, but higher than the Limon Group formations. The total species diversity range, however, was the greatest in this study.

The lowermost samples examined in Section 19 (Appendix B, PPP 61, 371–374) contain *Sphaeroidinellopsis* sp., *Globorotalia margaritae, Globigerina nepenthes* and a rare occurrence of *Globorotalia puncticulata.* The age of this lower part of the Cayo Agua Formation appears to be ~4.0 Ma using the extinction of *Globigerina nepenthes* at 4.0 Ma and the fact that *Globorotalia puncticulata* did not migrate into the Caribbean earlier than 4.0 Ma (Dowsett, 1989; note: based on this, *G. puncticulata* does not appear at DSDP site 502 until approximately 3.4 Ma, at the boundary between the Gauss and the Gilbert chrons). In the uppermost samples of Section 19 (PPP 335–338), key taxa include *Dentoglobigerina altispira, Globigerinoides conglobatus, G. obliquus* (significantly dominant relative to *G. ruber*), *Sphaeroidinellopsis* sp. and *Globorotalia plesiotumida.* The age range for the top of the formation is 5.3–3.5 Ma using the FAD of *G. conglobatus* and the date of 3.5 Ma when *G. ruber* becomes dominant relative to *G. obliquus* in the Caribbean (disregarding *Globorotalia plesiotumida* due to its lower confidence, which would suggest a minimum age of 4.0 Ma).

Key calcareous nannofossil taxa identified include *Sphenolithus abies, Reticulofenestra pseudoumbilicus, Pseudoemiliania lacunosa* and *Ceratolithus acutus.* The co-occurrence of *S. abies* and *P. lacunosa* (PPP 371–374) indicates an age of 3.6–3.5 Ma; however, *C. acutus* (5.0 to 4.6 Ma) was found in a sample near the base of the Cayo Agua (at PPP 61) and provided an age estimate for the lowermost Cayo Agua Formation for Coates *et al.* (1992). On the other hand, the sample with *C. acutus* also contains a large number of reworked planktic foraminifera, implying that *C. acutus* too, may be reworked.

In summary, the planktic foraminifera constrain the top of Cayo Agua to 5.3–3.5 Ma based on the dominance of *G. obliquus* relative to *G. ruber* and the occurrence of *G. conglobatus*. The base is restricted to ~4.0 Ma based on the co-occurrence of *Globorotalia puncticulata* and *G. nepenthes*. Nannofossil data for the base indicate both older and younger dates relative to the planktic foraminiferal data; 3.6–3.5 Ma by the co-occurrence of *S. abies* and *P. lacunosa* and 5.0–4.6 Ma by the presence of *Ceratolithus acutus* (if it is not a product of re-working). Based on the same microfossil occurrences (listed above), graphic correlation analysis (Dowsett and Cotton, 1996) concluded that the uppermost Cayo Agua is 3.51 Ma and the base 5.03 Ma.

### *Escudo De Veraguas Formation*

The Escudo de Veraguas Formation crops out along the north and southeast coasts of the island of Escudo de Veraguas (Map 4, Appendix A), which lies due east of the Valiente Peninsula. These Late Pliocene sediments are the youngest of the Bocas del Toro Group. Planktic foraminifera were identified from thirteen samples of the Escudo de Veraguas Formation (PPP 168–170, 358, 360–362, 364–369; Table 2). Their relative stratigraphic positions are plotted in Sections 10–11, Appendix B.

The general character of the fauna in the Escudo de Veraguas Formation is an overwhelming dominance of *Globigerinoides ruber* and *G. sacculifer*, with *Globorotalia* spp. subdominant. The total species diversity for the Escudo de Veraguas Formation ranged from 6 to 19 per sample with a mean of 11, which is the lowest value for the Bocas del Toro Group, but higher than the Limon Group formations. The globorotaliids found in abundance in the main (North coast) section of this formation (*Globorotalia miocenica* and *G. pseudomiocenica*) were not found in the other sections of this study (except one occurrence of the latter in the Nancy Point Formation), which suggests different oceanic conditions at this locale.

Key planktic foraminifera for biochronology in the Escudo de Veraguas Formation include *Globigerinella calida*, which Bolli and Saunders (1985) considered indicative of the Pleistocene. However, Kennett and Srinivasan (1983) showed this species to range down into the Lower Pliocene. The only globorotaliid in the southeast section (PPP 168–170) is *Globorotalia crassaformis* (FAD = 4.3 Ma), which occurs in low numbers. *Pulleniatina obliquiloculata* was identified at PPP 168 and suggests a post-2.2-Ma age based on its reappearance in the Atlantic (Saito, 1976; Keigwin, 1982). Samples (PPP 360–369) in the middle and lower north section are characterized by abundant *G. miocenica* (LAD = 2.2 Ma) and *G. pseudomiocenica*, which indicates a minimum date of 2.2 Ma. Other key taxa include *Globigerinoides obliquus* (LAD = 1.8 Ma) in all samples, *Globorotalia tosaensis* (FAD = 3.1 Ma) *and Sphaeroidinella dehiscens* (FAD = 3.0 Ma) at PPP 362 (middle section), and *G. truncatulinoides* (FAD = 1.9 Ma) at PPP 360 (upper section).

One notable difference between the faunas of the Escudo de Veraguas Formation and the other Bocas del Toro formations (Cayo Agua, Shark Hole Point and Nancy Point) is the increase in the numbers of *Globigerinoides ruber* relative to *G. obliquus*. The switch from *G. obliquus*-dominant *to G. ruber*-dominant faunas occurs at DSDP site 502A between 3.5 and 3.0 Ma (Text-fig. 2), which supports ages of ≤ 3.5 Ma for the Escudo de Veraguas Formation.

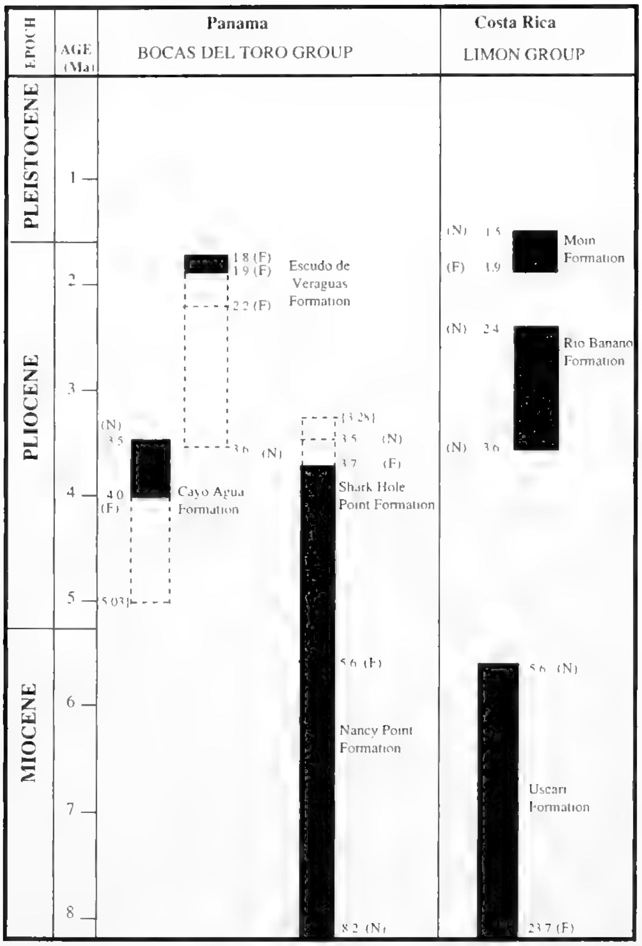
Nannofossils were abundant in this formation in general. The key taxa near the top were the small *Gephyrocapsa* spp. (FAD = 2.5 Ma) and *Calcidiscus macintyrei* (LAD = 1.5 Ma), which restrict the age to between 2.5–1.5 Ma. Near the base of the formation key taxa include: *Sphenolithus abies* (LAD = 3.5 Ma), *Pseudoemiliania lacunosa* (3.6–0.5 Ma), *Discoaster brouweri* (LAD = 1.9 Ma) and *D. pentaradiatus* (LAD = 2.5 Ma), which restrict the age to between 3.6–3.5 Ma.

To summarize the biostratigraphic data for Escudo de Veraguas, the planktic foraminifera suggest 1.9–1.8 Ma near the top, and possibly as old as 3.5 Ma at the base. The nannofossil data indicate assignment to Zone NN18 (age estimate: 2.2–1.9 Ma) designation for the top and an upper Zone NN15 (age estimate: 3.6–3.5 Ma) assignment for the base.

## REGIONAL CORRELATION

Correlations between formations described in this study and other Neogene marine deposits of the Caribbean region were made in the following manner. Age designations based on a particular zonal scheme were converted to a numerical framework based on the Neogene time scale of Berggren *et al.* (1985). Dates based on LADs and FADs of taxa were altered to currently accepted LADs and FADs based on Berggren *et al.* (1985) and Dowsett (1989). Studies which provided taxonomic data were critically assessed as to stratigraphic importance of key taxa. When possible, taxonomic consistency was maintained by viewing figured specimens and comparative material at the U. S. National Museum and the U. S. Geological Survey, Reston, Virginia. Text-figure 1 shows the localities of these eastern Pacific and Caribbean Neogene deposits, Text-figure 3 is an age chart of the formations analyzed herein, and Text-figure 4 is a correlation chart showing the relations among all of these land-based Neogene deposits.

The Neogene sediments found on the Pacific side of the southern Central American isthmus were studied

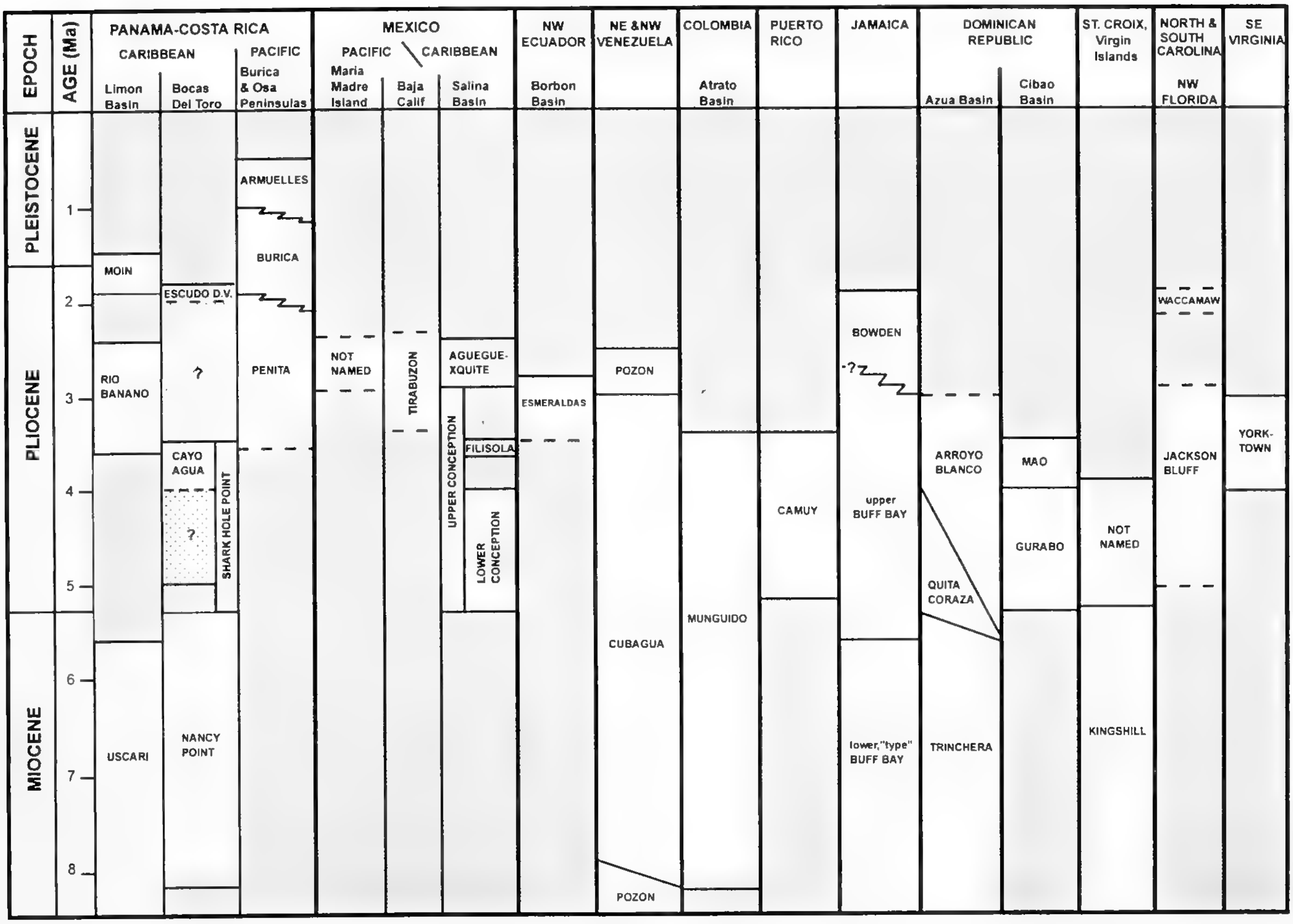


Text-figure 3.—Age chart of Caribbean, southern Central American formations, adapted from Coates *et al.* (1992). Dates with "N" or "F" next to them represent dates based on a nannofossil or foraminiferal datum, respectively. Dates in brackets represent age estimates made by graphic correlation analysis (Dowsett and Cotton, 1996)

by Coates *et al.* (1992), and a more detailed biochronology by Cotton (1991). The results are summarized as follows. The Charco Azul Group deposits occur on the Burica and Osa peninsulas of Panama and Costa Rica and were dated using planktic foraminifera and calcareous nannofossils. The Charco Azul Group consists of three formations: Penita, Burica and Armuelles. The Penita Formation is the oldest in the group and the planktic foraminifera were sparse and poorly preserved in general. The base of this formation could only be constrained to ≥ 3.5 Ma by *Sphaeroidinellopsis* (LAD = 3.0 Ma) and the calcareous nannofossil *Sphenolithus abies* (LAD = 3.5 Ma). Lowermost samples from the overlying Burica Formation provided a minimum age for the Penita Formation of 3.6–3.5 Ma based on the co-occurrence of *S. abies* and *Pseudoemiliania lacunosa* (3.6–0.5 Ma). This would make the Burica Formation partially coeval with the Rio Banano and Escudo de Veraguas formations. However, Cotton (1991) noted an absence of *Globigerinoides obliquus* (LAD = 1.8 Ma) throughout the Burica Formation, whereas *G. ruber* was consistently present. This evidence combined with left-coiled *Globorotalia menardii* (FAD = 2.2 Ma) suggest a Late Pliocene date of ≤1.8 Ma for a maximum age of the Burica Formation, which would make it coeval with the Moin and upper Escudo de Veraguas formations. The top of the Burica Formation and the base of the Armuelles Formation were dated at 1.7–1.5 Ma based on the presence of both large *Gephyrocapsa* spp. and *Calcidiscus macintyrei*. The minimum age for the Armuelles Formation was constrained to 0.5 Ma by the presence of *P. lacunosa* and absence of *C. macintyrei*. The Armuelles Formation is younger than the youngest Caribbean formation in this study, the Moin Formation.

Neogene marine sedimentary sequences have been studied in detail from two regions in the Dominican Republic: the Cibao Basin in the north (Saunders *et al.*, 1986) and the Azua Basin in the southwest (McLaughlin, 1989). In the Cibao Basin, the Mao Formation was dated as Zones NN14–15 (approximate age: 4.0–3.4 Ma), which correlates with the lower Rio Banano, Cayo Agua, and upper Shark Hole Point formations. The Gurabo Formation was dated as Zones NN12–13 (approximately 5.6–4.0 Ma), which correlates with the lower Shark Hole Point Formation and uppermost Nancy Point Formation.

In the Azua Basin, Dominican Republic, the Trinchera Formation was dated by McLaughlin (1989) from the base of the *Globorotalia menardii* Zone to the top of the *G. margaritae margaritae* Subzone (approximately 10.4–3.6 Ma). It is not apparent what species the base is defined by as the key species *G. mayeri* (LAD = 10.4) was not listed for this formation. However, *Globoquadrina dehiscens* (LAD = 5.3 Ma) co-occurs with *Globorotalia margaritae* (5.6–3.4 Ma) in the upper part of the formation, which gives it an age of 5.6–5.3 Ma. Therefore, the top of the Trinchera Formation correlates with the uppermost Nancy Point Formation. The Quita Coraza Formation was dated by McLaughlin (1989) from the middle of the *Globorotalia margaritae margaritae* Subzone to the top of the *G. margaritae* Zone, and (based on my interpretation) using the time scale of Berggren *et al.* (1985) this corresponds to approximately 5.15 to 3.4 Ma. *Globigerina nepenthes* occurs throughout this formation and suggests a minimum age of 4.0 Ma (Dowsett, 1989). *Globigerina nepenthes* co-occurs once with *Globorotalia margaritae*, which further restricts the minimum age to 5.6–4.0 Ma. The maximum age relies on the oc-



Text-figure 4.—Regional correlation chart comparing the Neogene sequences of this study to other formations of the Central American isthmus and in the Caribbean and eastern Pacific basins, based on studies mentioned in text.

currence of *Globigerinoides ruber* (McLaughlin, 1989, used a FAD of mid-Zone N18, approximately 5.15 Ma) in the underlying Trinchera Formation. This formation correlates with the lower Shark Hole Point Formation.

The youngest formation in the Azua Basin, the Arroyo Blanco Formation, was dated (McLaughlin, 1989) from the upper *Globorotalia humerosa* Zone through the *Globigerinoides trilobus-fistulosus* Zone (approximately 5.6–3.0 Ma). *Dentoglobigerina altispira* and *Sphaeroidinellopsis* sp. are the limiting taxa for the upper age estimate. The maximum date relies on the FAD of *Candeina nitida,* due to the absence of other data. This formation correlates with the Rio Banano Formation, and possibly the Cayo Agua, Shark Hole Point and Nancy Point formations, depending on the true base of the Arroyo Blanco Formation.

Bermudez and Seiglie (1970) identified planktic foraminifera from the Neogene Camuy Formation of Puerto Rico. They recorded *Sphaeroidinellopsis* sp. (LAD = 3.0 Ma), *Globorotalia margaritae* (5.6–3.4 Ma), *D. altispira* (LAD = 2.9 Ma) and *G. tumida* (FAD = 5.2 Ma), which indicate the age of 5.2–3.5 Ma. The Camuy Formation is correlative with the basal Rio Banano, basal Escudo de Verguas, Cayo Agua and Shark Hole Point formations.

Palmer (1945) was the first to identify numerous planktic foraminifera from the Bowden Formation of Jamaica. Included in her species list is *G. truncatulinoides* (FAD = 1.9 Ma), which would limit part of the Bowden to ≤1.9 Ma. *Globorotalia miocenica* (listed as a variety of *G. menardii),* which became extinct in the Latest Pliocene, is also listed. *Sphaeroidinella dehiscens* (FAD = 3.0 Ma) is also listed, which limits a portion of the Bowden to ≤ 3.0 Ma. Lamb and Beard (1972), however, did not find *G. truncatulinoides* below the Manchioneal Formation, which overlies the Bowden. Berggren (1993), in a detailed biostratigraphic analysis, identified *Globoquadrina dehiscens, Globigerina nepenthes, D. venezuelana,* and *Globorotalia* *margaritae* in the Bowden Formation, which is approximately Late Miocene to Early Pliocene and correlative with the upper Uscari, lower Rio Banano, lower Cayo Agua, Shark Hole Point and Nancy Point formations.

In the Buff Bay Formation of Jamaica, Lamb and Beard (1972) recorded *G. margaritae* (LAD = 3.4 Ma), *Sphaeroidinellopsis* sp. (LAD = 3.0 Ma), *Sphaeroidinella* sp. and *G. miocenica* in the upper portion, and *Globigerinoides conglobatus* (FAD = 5.3 Ma), *N. humerosa* and *N. acostaensis* in the lower, "type" Buff Bay. This puts a boundary of 3.4–3.0 Ma on the upper section and <5.3 Ma on the lower section. Also found in the lower Buff Bay was *Globoquadrina dehiscens,* which last occurs in the Late Miocene (LAD = 5.3 Ma). The lower, "type" Buff Bay correlates with the Nancy Point and the Uscari formations, while the upper Buff Bay is correlative with the lower Rio Banano Formation and possibly with the lower Escudo de Veraguas Formation.

Neogene sediments from the island of St. Croix, Lesser Antilles, yielded planktic foraminifera indicative of the Late Miocene and Early Pliocene (Lidz, 1982). Key taxa reported include *Globigerina nepenthes* (LAD = 4.0 Ma) in association with *Globigerinoides conglobatus* (FAD = 5.3 Ma), providing an age range of 5.3–4.0 Ma for some of the samples. *Globoquadrina dehiscens* (not found in Panama or Costa Rica) is recorded in numerous samples, indicating an age ≥ 5.3 Ma. Notably absent is *Sphaeroidinella* sp., while *Sphaeroidinellopsis* sp. is recorded frequently, supporting an age ≥ 3.0 Ma. *Globorotalia margaritae* is absent from these deposits despite the fact that its stratigraphic range overlaps with the age of these sediments, suggesting that environmental conditions were not conducive to *G. margaritae.* The deposits from St. Croix are correlative with the lower Shark Hole Point Formation and Nancy Point Formation.

Neogene deposits from the Caribbean side of the Isthmus of Tehuantepec, Mexico, were dated by Akers (1979, 1984), who identified key nannofossils and planktic foraminifera. Akers assigned Zone N20 to the Agueguexquite Formation, which contains *Sphaeroidinella* sp. (FAD = 3.0 Ma) and nannofossils *P. lacunosa* (FAD = 3.6 Ma) and *D. pentaradiatus* (LAD = 2.4 Ma), fixing the age between 3.0 and 2.4 Ma. The absence of *S. abies* (LAD = 3.5 Ma) supports this age. This formation is correlative with the Rio Banano Formation and possibly Escudo de Veraguas Formation. The Filisola Formation (Akers, 1979) contains no age-indicative planktic foraminifera; however, the co-occurrence of *P. lacunosa* and *S. abies* limits the age to 3.6–3.5 Ma. Planktic foraminifera identified from the Concepcion Inferior Beds (Akers, 1979) include *G. margaritae* (5.6–3.4 Ma), *Sphaeroidinellopsis* sp. (LAD = 3.0 Ma), and *Globigerinoides conglobatus* (FAD = 5.3 Ma), which yield an age of 5.3–3.4 Ma, but the same key nannofossil taxa occur as in the Filisola, restricting the age to 3.6–3.5 Ma. The Concepcion Superior Beds contain *Globigerina nepenthes* (LAD = 4.0 Ma) and *Globigerinoides conglobatus* (FAD = 5.3 Ma), constraining the age to 5.3–4.0 Ma. However, Akers also identified both nannofossil taxa *P. lacunosa* (FAD = 3.6 Ma) and *S. abies* (LAD = 3.5 Ma), which suggests a younger age. The Filisola, Concepcion Inferior and Concepcion Superior beds correlate with the Rio Banano, Cayo Agua, and Shark Hole Point formations and possibly the basal Escudo de Veraguas Formation.

In the eastern Falcon region, Venezuela, Blow (1959) reported numerous planktic foraminifera from the Pozón Formation, most of which are indicative of a Miocene age (*e.g., Globoquadrina dehiscens*). However, he also recorded *S. dehiscens* and *G. miocenica,* both indicative of the Late Pliocene. If these identifications are correct, the upper Pozón Formation correlates to the Rio Banano, Cayo Agua, and Shark Hole Point formations.

The Esmeraldas Formation of Ecuador yields well preserved, abundant planktic foraminifera which provided Hasson and Fischer (1986) with an age range of 3.5–3.2 Ma. However, in their table of species occurrences are *G. tosaensis* and *S. dehiscens*, which suggest younger dates. Hasson and Fischer discussed the discrepancy of *G. tosaensis* in the samples as its FAD = 3.1 Ma, and *S. dehiscens* has a FAD = 3.0 Ma. Further, *Globigerinoides ruber* is found in most of the samples while *G. obliquus* is found in less than half of the samples (Text-fig. 2). This supports the minimum age indicated by the above mentioned FADs of 3.0 Ma, to give an age of 3.5–3.0 Ma. The Esmeraldas is correlative with the Rio Banano Formation and possibly lower Escudo de Veraguas Formation.

Duque-Caro (1990) dated the Munguido Formation, in northwestern Colombia, as 3.4 Ma to Late Miocene Zone N17 based on *Globorotalia margaritae* (5.6–3.4 Ma) found near the top and *G. conomiozea subconomiozea* found at the base. The Munguido is correlative with the Cayo Agua, Shark Hole Point, upper Nancy Point, and lower Rio Banano formations.

The Neogene of Maria Madre island, off the Pacific coast of Mexico, was studied by Carreño (1985). She identified *Globigerinoides fistulosus* (FAD = 2.9 Ma), *S. dehiscens* (FAD = 3.0) and the nannofossils *P. lacunosa* (FAD = 3.6 Ma) and *D. pentaradiatus* (LAD = 2.4 Ma). These taxa provide an age of 2.9–2.4 Ma and are correlative with the upper Rio Banano Formation and possibly the lower Escudo de Veraguas

Formation. Carreño (1981) identified planktic foraminiferal faunas from the Neogene Tirabuzon Formation, Baja, California, and assigned a date of Early to middle Pliocene. This formation approximately correlates to the Rio Banano, Cayo Agua, and Shark Hole Point formations.

Dowsett and Wiggs (1992) showed that planktic foraminiferal faunas from the Yorktown Formation in southeastern Virginia support an age of 4.0–3.0 Ma based on the presence of *Sphaeroidinellopsis seminulina* (LAD = 3.0 Ma), *Dentoglobigerina altispira* (LAD = 2.9 Ma) and *Globorotalia puncticulata* (FAD = 4.0 Ma). These sediments correlate with the Rio Banano, Cayo Agua, and upper Shark Hole Point formations.

Akers (1972) analyzed planktic foraminiferal faunas from the Waccamaw Formation of North and South Carolina, and the Jackson Bluff Formation of southwestern Florida. The Waccamaw Formation yielded *G. truncatulinoides* (FAD = 1.9 Ma) and *G. obliquus* (LAD = 1.8 Ma) at one locale, which limits the age of at least part of the Waccamaw to 1.9–1.8 Ma. This portion of the Waccamaw, therefore, correlates to the Moin Formation of this study. Akers (1972) recorded the presence of *Sphaeroidinella* sp. (FAD = 3.0 Ma), *Sphaeroidinellopsis* sp. (LAD = 3.0 Ma), *G. margaritae* (5.6–3.4 Ma), *D. altispira* (LAD = 2.9 Ma) and *Globigerinoides conglobatus* (FAD = 5.3 Ma) in the Jackson Bluff Formation. The co-occurrence of *Sphaeroidinella* and *Sphaeroidinellopsis* in the same horizon/locality indicates an age of 3.0 Ma. *Globigerinoides conglobatus* co-occurring with *Globorotalia margaritae* at another locality restricts the age of that sample to 5.3–3.4 Ma. A third locality which contains *Sphaeroidinella* sp. and *D. altispira*, but not *Sphaeroidinellopsis* sp., is restricted to 3.0–2.9 Ma. The overall age assigned by Akers is Early Pliocene to early Late Pliocene. Thus the Jackson Bluff was deposited contemporaneously with the lower Rio Banano, Shark Hole Point and the Cayo Agua formations of this study.

## SUMMARY

Using planktic foraminifera (this study) and calcareous nannofossil data (Bybell, Chapter 2, this volume), I have established a biochronologic framework for the Neogene strata along the Caribbean coast of the southern Central American isthmus (Text-fig. 1).

In the Bocas del Toro Group, the oldest formation in the study, the Nancy Point Formation, is Late Miocene, between 8.2 to 5.3 Ma in age. The Shark Hole Point Formation overlies the Nancy Point Formation and is Early to mid-Pliocene, between approximately 5.3 and 3.7 Ma. The Cayo Agua Formation is contemporaneous with the Shark Hole Point Formation and is Early to middle Pliocene (between 4.0, possibly 5.0, and 3.5 Ma). The Escudo de Veraguas Formation is the youngest of the Bocas del Toro Group and is dated as middle to Late Pliocene (between 2.2, possibly 3.5, and 1.8 Ma).

In the Limon Group, the uppermost Uscari Formation is dated as Late Miocene (between 7.7–5.6 Ma) from this study; previous studies indicate that the base is Early Miocene (23.7 Ma). The Rio Banano Formation is dated as middle to early Late Pliocene (3.6 to 2.4 Ma). The Moin Formation is dated as uppermost Pliocene to Lower Pleistocene (1.9 to 1.5 Ma).

Mean species diversity of planktic foraminifera per sample in the Bocas del Toro Group decreases from the oldest (16 species) to the youngest (11 species) formation, which coincides with an increasingly emergent isthmus. Evidence from benthic foraminifera (Collins, 1993; Collins *et al.*, 1995) suggests a general shallowing from the Nancy Point Formation to the Escudo de Veraguas Formation. Faunal diversity in the Limon Group is lower than the Bocas del Toro Group with a mean species diversity of 7 species, compared to 13 for Bocas del Toro.

The frequently found co-occurrence of *Sphenolithus abies* and *Pseudoemiliania lacunosa* in this study implies that during the 100,000 year period between 3.6 Ma and 3.5 Ma there was a widespread sedimentation event which was preserved extensively in both the Limon and Bocas del Toro basins, as well as other locales in the Caribbean Basin (*e.g.,* Akers, 1979, 1984). The 3.6–3.5 Ma period corresponds to a eustatic sea-level rise of approximately 60 m, the TB3.6 sea-level cycle of Haq *et al.* (1987), dated as 3.8–2.9 Ma. The Atlantic Coastal Plain Model of Krantz (1991) also documented a sea-level rise between 4.0 Ma and 3.3 Ma. An alternative explanation to this phenomenon is that one or more of the accepted LADs and FADs for these two species may not be applicable in these shallow, nearshore deposits. *Pseudoemiliania lacunosa* may have originated earlier than 3.6 Ma or *S. abies* may not have become completely extinct at 3.5 Ma. Global diachrony in first and last appearances of Late Neogene planktic foraminifera and nannofossils was demonstrated by Dowsett (1988, 1989), among others, and diachrony may exist between deep-sea occurrences and those on the continental shelf.

The age restrictions placed on the Neogene sediments examined in this study aid in geologic investigations of the Central American isthmus, especially those related to the history of its emergence, temporal shifts in its faunal assemblages, and evolutionary and ecological changes of marine organisms living adjacent to the isthmus. The biochronology provided in this study also contributes to the regional correlation of Neogene deposits in the Caribbean and eastern Pacific basins.

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# CHAPTER 4

# A PALEOENVIRONMENTAL ANALYSIS OF THE NEOGENE OF CARIBBEAN PANAMA AND COSTA RICA USING SEVERAL PHYLA

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## INTRODUCTION

The Neogene sedimentary environments of the Panama Canal, Bocas del Toro, and Limon basins were controlled by local and basin-wide Caribbean oceanographic conditions, regional tectonic movements, changes in sea level, and seafloor topography. Through the approximately 9 million years spanned by the sediment samples of the Panama Paleontology Project (PPP) examined in this study, only a few large-scale oceanographic and tectonic changes can be discerned above the "noise" of the more locally expressed controls. Local paleoenvironments, determined at the level of individual sedimentary samples to formations, are interpreted by members of the PPP from four taxonomic groups: benthic foraminifera, corals, ostracodes and teleost fish. The data from this diverse array of taxa are used to summarize the depositional histories of the three Neogene basins.

One of the most important contributions of paleoenvironmental analyses to the PPP is that all of the paleobiologic data can be identified and compared within the framework of space and habitat, as well as time. Data on taxonomic occurrences of marine organisms used in studies of biodiversity, evolution (origination and extinction), biogeography and ecology begin by defining as precisely as possible their environment and their chronologic position. To make valid comparisons of taxa from different habitats, environment must be held constant to standardize the results and reduce sampling bias. For example, an analysis of Pliocene changes in the ecological structure of southern Central American mollusks would be meaningless if early Pliocene inner neritic and late Pliocene outer neritic taxa were compared. Inner and outer neritic faunas would be expected to differ without any change in time. Environmental bias is often not a problem with studies of change through time at large chronologic or geographic scales, such as for all Paleozoic shelf faunas or global biodiversity, but when faunal changes are examined at the relatively fine scale targeted by the PPP to unravel evolutionary histories and examine biogeographic changes, paleoenvironmental analyses become critical to standardizing faunal occurrence data.

Paleoenvironmental studies are also valuable geologically for interpreting tectonic changes and the stratigraphy of paleobasins. For example, when paleoenvironments are expressed as water depths, the paleobathymetric changes can be partitioned into tectonic and eustatic components, and rates of subsidence and uplift can be calculated (Collins *et al.*, 1995). The large-scale structure of paleobasins can also be determined from the paleobathymetry, from hydrographic data such as oxygen content infered from paleofaunas, and from the biogeographic affiliations of the faunas.

Four taxonomic groups were used to interpret Neogene paleoenvironments of Caribbean Panama and Costa Rica:

1. *Benthic foraminifera,* which are part of the meiofauna, are the most commonly used fossils for analyzing Cenozoic paleoenvironments because of their great abundance and diversity, their presence in virtually all marine-influenced environments, and the extensive knowledge of their ecology.

2. *Ostracodes,* which are found in marine, brackish, hypersaline and freshwater habitats, are the next most frequently used taxon. This is probably a result of lower abundances rather than individual taxa having larger environmental ranges. Furthermore, studies of environmental distributions of modern ostracodes of the Gulf of Mexico and Caribbean region have lagged behind studies of modern assemblages elsewhere, such as Europe.

3. *Otoliths* (fish earbones) are widely distributed and often abundant in PPP sediment samples. Because they are not as abundant as benthic foraminifera and ostracodes, have fewer taxonomic experts, and are commonly identifiable only to the genus level, they have traditionally been less useful for paleoenvironmental analysis. However, although their originally pelagic habit results in wider geographic distributions of taxa, they are shown herein to be a powerful complementary tool in determining paleobathymetry for most of the formations analyzed.

4. *Scleractinian corals* that lack symbiotic zooxanthellae are usually not associated with reefs and live in a wide range of depths and temperatures. They are the least abundant and diverse taxon employed in this study (having only about 12 extant cosmopolitan species), but have also proved useful for paleoenvironmental analysis. As with the other three taxa, their species distributions can be described by ranges in water depths. Ahermatypic corals occur down to 6300 m and geographic ranges are wider with increasing depth, so relatively shallow taxa, such as those reported herein, are commonly confined to one side of an ocean basin, *e.g.*, the tropical Western Atlantic.

Mollusks, including bivalves, gastropods and cephalopods, are quite useful for paleoenvironmental determinations. However, they are not included in this chapter because the necessary ecological studies of this vast tropical fauna have not been done.

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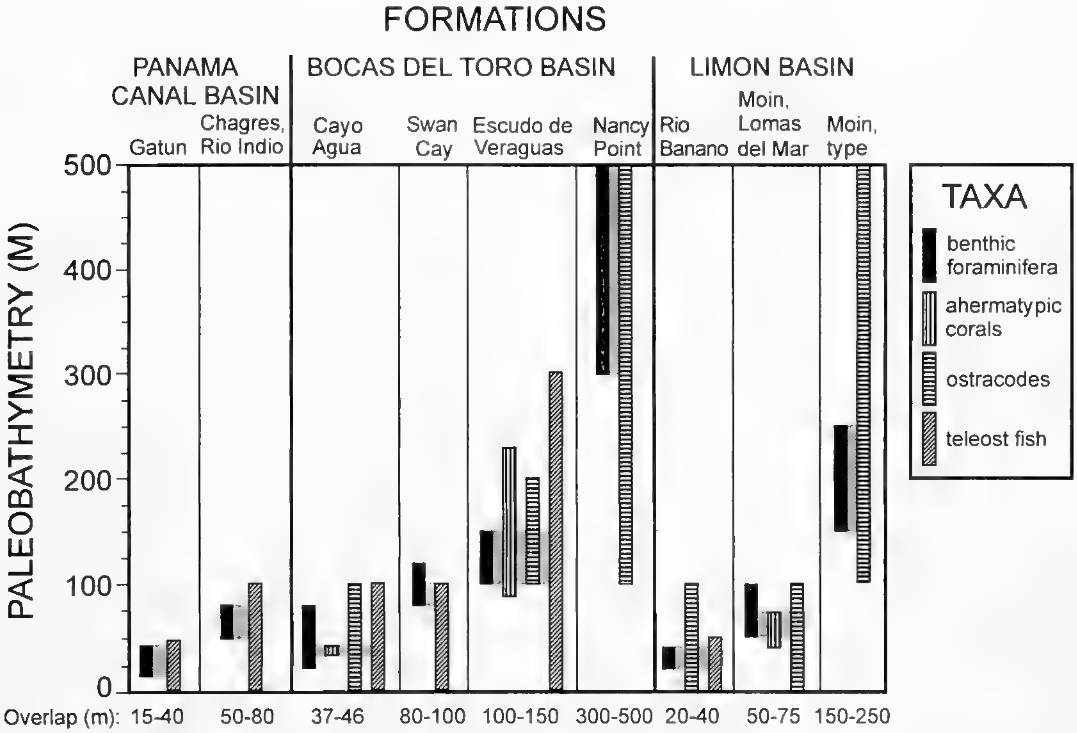
## COMPARISON OF METHODS USED FOR DIFFERENT TAXA

The methods employed in specimen preparation and paleoenvironmental determinations are described in more detail by Collins (benthic foraminifera, this volume), Aguilera and Aguilera (teleost otoliths, this volume), Borne *et al.* (ostracodes, this volume), and Cairns (ahermatypic corals, this volume). Below, we summarize briefly the similarities and differences in their paleoenvironmental methods and uses.

For the benthic foraminiferal analyses, ecological relationships of modern species of the Caribbean Sea and Gulf of Mexico are applied to their fossil counterparts mainly in terms of ranges in water depths (but see Collins, this volume, for ranges in terms of habitat). Depth itself is not an ecological control, but rather, a proxy for a combination of correlated environmental parameters that generally vary consistently within, and even between, oceanic basins. About 90% of the species that are common (*i.e.*, occur at ≥1% frequency in at least one sediment sample) in the Bocas del Toro and Limon groups are extant. For extinct taxa, depth ranges are determined through their association with extant species in fossil sediments of the tropical American region.

The techniques used for interpreting paleoenvironments are most similar for ostracodes and benthic foraminifera. In this study, species-level data for these fossils are compared to modern distributions of the same species found within the same Caribbean ocean basin, and separate depth determinations are made for each sample from a collecting site, which has a PPP number. As with benthic foraminifera, most ostracode species are still living; approximately 76% of identified ostracode species of the Limon Group, Caribbean Costa Rica, are extant. The techniques differ in two ways. First, benthic foraminiferal interpretations are based on the deepest dwelling taxa (to allow for possible downslope redeposition of sediments) using the overlap of the species' paleobathymetric ranges, whereas ostracodes use the overall similarities between Recent and fossil faunas. Second, relative abundances



Text-figure 1.—Paleobathymetric comparison of members or formations (columns) of the Panama Canal, Bocas del Toro, and Limon basins using four different taxa. Shading denotes the overlap in depth ranges shown across the bottom.

were used in the foraminiferal analyses, whereas the presence *vs.* absence of taxa was used for ostracodes.

The use of paleoenvironmental methods with ahermatypic corals is similar to those with microfossils in that they are at the species level and use the overlap of bathymetric ranges. However, specimens are too large and sparsely distributed to make determinations for single samples, so bathymetric ranges of taxa from multiple samples of each formation or section are combined into one paleoenvironmental analysis. This method carries the assumption that the depositional environment did not change within the formation/section, which was generally supported in this case by previously published results for separate samples (Collins *et al.*, 1995). Extinct taxa in the analyses (only about 20% of the ahermatypic coral species are extant) were compared to closely related living species for about 30% of the taxa.

Paleoenvironmental analysis of teleost otoliths was standardized by Nolf and Brzobohaty (1992) and differs from the methods used for the other taxa. Taxonomic identifications of fish from otoliths are generally at the generic level. Approximately 98% of the fossil genera are extant. Relative abundances of genera are calculated per 100-m-depth interval and the interval in which the most genera peak is considered the most likely depositional environment. If several peaks occur, reworking or some other process is implied and the results have less confidence. Otoliths, like ahermatypic corals, are too sparsely distributed in sediments to calculate paleobathymetries for single samples, so genera found within a formation or other stratigraphic unit are combined into one analysis.

## PALEOENVIRONMENTAL DATA

### TRENDS IN PALEOENVIRONMENTAL DETERMINATIONS FROM DIFFERENT TAXA

A side-by-side comparison of paleoenvironmental determinations from benthic foraminifera, ostracodes, ahermatypic corals and otoliths indicates the extent to which they agree. Text-figure 1 plots paleobathymetries determined from the different taxa at the finest stratigraphic level at which they can all be compared: either biofacies, members or formations. Results from different taxa support each other quite well. For all stratigraphic units, the paleodepths from different taxa overlap each other. Except for possible prior knowledge of the previously published benthic foraminiferal results, each paleontologist worked independently. Even if the benthic foraminiferal results are excluded, the remaining water depth ranges overlap.

To some extent, the differences in results (Text-fig. 1) mirror the differences in the methods and the taxonomic level of identification. The benthic foraminiferal paleobathymetric ranges always overlap those of another taxon and are commonly the most constrained. In ⅔ of the cases, the benthic foraminiferal range defines the complete range overlap. Benthic foraminifera tend to fall at the deeper end of the ranges of the other taxa, as happens with the Gatun Formation, Rio Indio biofacies of the Chagres Formation, Nancy Point Formation, Swan Cay Formation, and Lomas del Mar Member of the Moin Formation. This is at least partly because paleodepths based on benthic foraminifera emphasize the shallowest ranges of the deepest dwelling taxa to compensate for possible downslope transport, which would tend to bias paleodepths toward deeper values. Depth ranges from ostracodes and teleost fish always overlap and generally extend beyond those of the benthic foraminifera at both the shallow and deep ends. In the case of ostracodes, this may be because estimates are based on presence/absence of species rather than relative abundance, their depth preferences are less well studied, the planktic species are more mobile, and/or proportionately fewer species are still extant. In the case of teleost fish, it may be because depth ranges of genera are wider than individual species and/or because planktic taxa are generally more widespread than benthic ones. Ahermatypic coral ranges overlap the other ranges in all three instances.

Applying the modern depth ranges of four different taxa (each with its own analytic method) to paleodepths of stratigraphic units results in paleoenvironmental interpretations with a high degree of confidence. How constrained the depths are depends on the approach used to arrive at consensuses. Estimating the paleodepth of each formation based on the union of all taxonomic ranges gives the highest degree of confidence but the lowest resolution. Paleodepth estimates based on the intersection (overlap) of the ranges (Text-fig. 1, bottom) give the highest resolution and a lower degree of confidence, but one that is higher than any estimated from a single taxon. These comparisons are based at the levels of formations, members or biofacies, but Table 1 presents all paleoenvironmental determinations at a finer scale, for PPP sections on the Caribbean side of the Isthmus of Panama (App. B, this volume).

## COMPARISON OF PALEOENVIRONMENTS FROM THE CARIBBEAN COASTAL BASINS

The main Neogene sedimentary basins of the Caribbean side of southern Central America are, from east to west, the Panama Canal, Bocas del Toro, and Limon basins (Coates, this volume). They are dissimilar in their geographic spread, local to regional tectonic influences, and thickness of sediments. The Panama Canal Basin of central Panama (App. A, Maps 1–2, this volume) contains Eocene (Stewart and Stewart, 1980) to Upper Miocene, marine and terrestrial sediments, and as late as 6 Ma the basin connected Caribbean and tropical Pacific surface waters (Collins *et al.*, 1996a). The Panama Paleontology Project has examined the upper Middle to Upper Miocene Gatun Formation and the Upper Miocene Chagres Formation. Benthic foraminifera and otoliths (Text-fig. 1) show the siliciclastic sediments of the Gatun Formation to be nearshore to middle neritic (Table 1, Sections 1–2, 6). Benthic foraminifera of the Chagres Formation indicate that the sediments were deposited in deep water (Table 1, Sections 3–4). However, its Rio Indio biofacies reflects a much shallower depth (Text-fig. 1; Table 1, Section 5; Appendix A, Map 1) according to the benthic foraminifera (50–80 m) and otoliths (<100 m).

The Panama Canal Basin was episodically an interoceanic strait. In the Early Miocene, Pacific and Caribbean waters mixed to bathyal depths, as shown by depth preferences of benthic foraminifera from the La Boca Formation (Blacut and Kleinpell, 1969). With the late Middle Miocene deposition of the Gatun Formation, waters had shallowed to the point that the strait was closed, as indicated by the 84-m elevation of the lowest-lying Pacific-Caribbean passageway in the region, and by the biogeography of the benthic foraminifera, which are Caribbean to cosmopolitan in oceanic affiliation. By 6 Ma, basinal waters had deepened to upper bathyal depths to allow Pacific inflow, as indicated by the paleobathymetry and oceanic affiliation of benthic foraminifera from the Chagres Formation (Collins *et al.*, 1996a). Late Miocene sea level rise cannot account for the large (approximately 200-m) increase in water depth, so some tectonic event must have been the cause. The central Panama region was apparently tectonically quiescent in Late Miocene time (de Boer *et al.*, 1988), but fault blocks in the Panama Canal Basin (Mann and Corrigan, 1990) may have dropped to produce the Late Miocene reopening of the strait. The shallower Rio Indio biofacies of the Chagres Formation (Table 1, Section 5) delimits the western edge of the deep-water strait.

The paleoenvironmental history of the back-arc Bocas del Toro Basin of western Panama (Appendix A, Maps 4–9) can be traced from Early Miocene, deep-water sediments (Appendix B, Section 12) that formed the earliest Isthmus of Panama. Coastal sections of both the Bocas del Toro Basin and Limon Basin (see below) typically expose a sequence comprised of Upper Miocene bathyal sediments, Pliocene neritic sediments and Lower Pleistocene coral reefs (Appendix B, Section 25). Although most composite sections (Table

Table 1.—Paleoenvironmental information for geologic sections (Appendix B) of the Panama Canal, Bocas del Toro, and Limon basins. Superscripts refer to the following references: [1] Collins, 1993; [2] Collins *et al.*, 1995; [3] Collins *et al.*, 1996a; [4] Collins in Jackson *et al.* (this volume); [5] Cairns (this volume); [6] Borne *et al.* (this volume); [7] Aguilera and Aguilera (this volume); [8] Coates (Appendix B, this volume). References 5, 6 (in part), and 7 determined paleoenvironments for members or formations rather than sections, and are cited where samples from those sections were included. Paleoenvironments pertain to whole geologic sections except where intervals of vertical thickness are specified. The most constrained paleodepth ranges, equal to the overlap of individual determinations, are cited.

| Sec. No. | Section name (interval, m) | Paleodepth (m) | Additional descriptors |
|---|---|---|---|
| PANAMA CANAL BASIN AND NORTH COAST OF PANAMA | | | |
| 1[3,4,7] | Sabanita to Payardi | 15–40[4] | |
| 2[3,4] | Margarita to Gatun | 10–40[4] | |
| 3[3] | Toro Point | 200–500[3] | Pacific influence[3] |
| 4[3] | Piña | 200–500[3] | Pacific influence[3] |
| 5[3] | Indio River | 50–80[3] | |
| 6[3,7] | Miguel de la Borda, 1 km to the East | ~25[3] | |
| BOCAS DEL TORO BASIN | | | |
| 10[1,5–7] | Escudo de Veraguas, Northern Coast | 100–150[1] | muddy[1] |
| 11[1,5,6] | Escudo de Veraguas, Southeastern Coast | 100–150[1] | carbonate shoal/reef influence[1] |
| 12[1,4,7] | Valiente Peninsula, Bruno Bluff to Plantain Cays | | |
| | (1957–1937) | 150–200[1] | Bruno Bluff Mbr. |
| | (1780–1615) | 100–200[4,7] | Shark Hole Point Fm., possible coastal upwelling |
| | (1607–1428) | 200–500[7] | upper Nancy Point Fm. |
| | (1245–1168) | 300–500[1,7] | lower Nancy Point Fm. |
| 14[4] | Valiente Peninsula, Toro Cays | 60–100[4] | |
| 15[4] | Valiente Peninsula, Southern Coast (421) | 150–300[4] | |
| | (0) | 100–200[4] | |
| 16[1,5–7] | Cayo Agua, Norte Point, Western Side | 20–40[1] | proximal carbonate shoals/reef[1] |
| 17[4,5,7] | Cayo Agua, Piedra Roja Point, Western Sequence | 10–75[4] | proximal carbonate shoals/reef[4] |
| 19[1,4–7] | Cayo Agua, Norte Point to Tiburon Point (293–264) | 20–70[4] | proximal carbonate shoals/reef[4] |
| | (54-0) | 40–80[1] | proximal carbonate shoals/reef[1] |
| 20[6,7] | Cayo Agua, South of Nispero Point | | inner-middle shelf[6] |
| 22[4,7] | Bastimentos Island, Fish Hole, Eastern Sequence | 40–100[4] | proximal carbonate shoals/reef[4] |
| 23[4,7,8] | Bastimentos Island, Fish Hole, Western Sequence (11–2.6) | 75–100[4] | |
| | (2.6-0) | 40–100[4] | proximal coral reef[4,8] |
| 25[4,7,8] | Swan Cay, North of Colon Island | 80–120[4,7] | coral reef[4,8] |
| 26[8] | Colon Island, Hill Point | | coral reef[8] |
| LIMON BASIN | | | |
| 27[2,7] | Sandbox River | ~200[2] | continental shelf edge[2] |
| 28[2] | Carbon Dos (Dindiri) | 300–500[2] | |
| 29[2,6,7] | Banano River | 20–40[2] | proximal carbonate shoals/reef[2] |
| 31[4] | Bananito River | <100[4] | |
| 32[2,6] | Santa Rita | 20–40[2] | proximal carbonate shoals/reef[2] |
| 33[6,8] | Chocolate to Buenos Aires (665–557) | 1–9[6] | carbonate[6], coral reef[8] |
| 34[4,6,8] | Empalme (65–108) | 10–30[4] | coral reef[8] & restricted nearshore[6] |
| 36[2,5–8] | Lomas del Mar, Eastern Sequence | 50–73[2,5] | coral reef[2,8] |
| 37[2,6] | Lomas del Mar, Western Reef Sequence | 150–250[2] | possible coastal upwelling[6] |
| 38[4,6,8] | Lomas del Mar, Western Reef Track Sequence | 50–100[4] | coral reef[4,8] |
| 39[4] | Vizcaya River | 0–25[4] | |

1, Sections 10–11, 14–15, 17, 20, 22–23, 25, 26) include no biochronological changes, the few that do transit geologic time shallow upwards. The thick, northern Valiente Peninsula coastal section (Appendix A, Map 5) extends from the Upper Miocene Nancy Point Formation to the middle Pliocene Bruno Bluff Member of the Shark Hole Point Formation. Ostracodes of the Nancy Point Formation indicate outer neritic to upper bathyal deposition, whereas benthic foraminifera give the more constrained, upper bathyal depth (Text-fig. 1). Benthic foraminifera of the Bruno Bluff Member indicate an outer neritic paleodepth (Table 1, Section 12). All taxa (Text-fig. 1) indicate an inner to middle neritic depositional setting for the Cayo Agua Formation, on the small island of Cayo Agua (Appendix A, Map 6). Ahermatypic corals show the most constrained, middle neritic paleodepth. Benthic foraminifera show a carbonate shoal or reef influence and some shallowing from the early Early Pliocene (Table 1, Section 19) to late Early Pliocene (Table

1, Section 16). The Escudo de Veraguas Formation (Appendix A, Map 4) does not reflect any measurable change in water depth through time, but exposures along the southern coast (Table 1, Section 11) show a stronger carbonate shoal to reef influence than the northern coastal section (Table 1, Section 10). All paleobathymetric estimates, except for the otolith determination, which spans 0–300 m, support outer neritic depths (Text-fig. 1).

Coral reefs and reef-associated sediments of Bocas del Toro are primarily Upper Pliocene (Table 1, Sections 22, 26) to Pleistocene (Table 1, Section 25). Reefal deposits of the Pleistocene Swan Cay Formation (Text-fig. 1) were relatively deep, as indicated by the benthic foraminifera and supported by the otoliths, with paleodepth ranges overlapping at 80–100 m. Although the Middle Miocene Valiente volcanics contains both hermatypic reef patches and ahermatypic corals, they are patchy and small in scale and diameter, and there appears to be an increasing abundance of larger scale reefs through time in the region. The pattern of an increasing occurrence of reefs is consistent with the hypothesis of an increasing carbonate regime in the Caribbean during the Late Miocene to Pliocene, associated with the progressive constriction of the Pacific-Caribbean seaway (Collins *et al.,* 1996b).

Sediments of the Limon Basin, Costa Rica (Appendix A, Maps 10–11) were also deposited in a back-arc volcanic setting. The basin contains Upper Oligocene, carbonate-bank sediments that underlie bathyal siliciclastics of the thick, uppermost Oligocene to Upper Miocene Uscari Formation (Cassell and Sen Gupta, 1989a; Collins *et al.,* 1995; Appendix A, Map 10; Table 1, Sections 27, 28). Upper Pliocene to lowermost Pleistocene sediments are exposed in relatively thin sections (Coates, this volume) and have a strong carbonate shoal to reef influence (Table 1, Sections 29, 32–34, 36–38). The Rio Banano and Moin formations span measurable geologic time and display varying facies in different exposures, but paleowater depths within their composite sections did not change measurably. The Rio Banano Formation (Appendix A, Inset C of Map 11; Table 1, Section 29) exposes a predominantly siliciclastic facies at Quitaria, whereas the type section at Bomba (Cassell and Sen Gupta, 1989b) shows a strong carbonate shoal to reef influence. Benthic foraminifera, ostracodes and otoliths all indicate an inner to middle neritic setting, although the benthic foraminifera suggest the more constrained range of 20–40 m. The Moin Formation includes extremely different paleoenvironments. Sediments of the type Moin section (Table 1, Section 37), exposed along an unnamed creek in the El Cangrejo community (Appendix A, Inset B of Map 11), were deposited in relatively deep water near the shelf edge, as indicated by benthic foraminifera and ostracodes (Text-fig. 1), possibly within an area of coastal upwelling (Borne *et al.,* this volume). Up the steep hill from this exposure and forming one in a series of coral-reef ridges (Taylor, 1973, 1975) are the in-place coral reefs (Table 1, Sections 36, 38) of the Lomas del Mar area, also included within the Moin Formation. Paleoenvironmental determinations using benthic foraminifera, ahermatypic corals and ostracodes, which have an overlapping paleobathymetry of 50–75 m (Text-fig. 1), indicate that the coral reefs were relatively deep.

The Bocas del Toro and Limon basins have the same general back-arc setting and history of uplift, but sedimentation patterns and some microfaunas indicate dissimilar paleoenvironments for the same ages and water depths. Similar Pliocene to Recent patterns of tectonic uplift between the two basins are indicated by covarying rates of coastal emergence and increased rates of Pleistocene to Recent uplift caused by the arrival of the subducted Pacific Cocos Ridge at the Caribbean coast (Collins *et al.,* 1995). Sediment sources differed. Sediments of the Rio Banano Formation, derived from erosion of the Cordillera de Talamanca, formed a thick deltaic wedge that was part of the Miocene to Recent, broad coastal fan system of Costa Rica to southern Nicaragua (Sheehan *et al.,* 1990). Coeval deposits of the Bocas del Toro Basin have no such facies, and faunas also differed. Cluster analyses of benthic foraminifera (Collins *et al.,* 1995) and ostracodes (Borne *et al.,* this volume) generally group assemblages with similar ages and environments, but within these large clusters, benthic foraminiferal assemblages separate completely the uppermost Miocene, upper bathyal Nancy Point Formation of Bocas del Toro and Uscari Formation of Limon. They also distinguish the middle Pliocene, inner to middle neritic Cayo Agua Formation of Bocas del Toro and Rio Banano Formation of Limon. Additionally, oxygen isotopes of mollusks from the same ages and paleodepths, but from the two different basins, exhibit different ranges in $\delta^{18}O$, suggesting that marine conditions in the two basins were different (Terranes *et al.,* 1996).

## SUMMARY

1. Paleoenvironmental methods among the four taxonomic groups differ, mainly in the level of taxonomic and stratigraphic units considered. Benthic foraminifera and ostracode methods are based on species and sediment samples, the ahermatypic coral method uses species and members to formations, and the teleost otolith method uses genera and members to formations. The differences in methods are reflected in the differences in results to some extent.

2. Nonetheless, results of the paleoenvironmental interpretations using four different taxa overlap each other in all formations studied, resulting in more constrained and confident estimates of paleodepths than with a single taxon.

3. Neogene environmental histories among the three basins differed. The Panama Canal Basin was a shallow, Middle Miocene, Caribbean basin until deepening about 6 Ma caused an inflow of deep, Pacific water. The Bocas del Toro and Limon basins were alike in their back-arc tectonic setting, histories of uplift, and sequence of sediments: bathyal Miocene, neritic Pliocene and lower Pleistocene coral reefs. The two basins differed in sediment source and coeval, isobathyal microfaunas.

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# PART 2

# PALEOBIOTIC SURVEY

# CHAPTER 5

# THE MIOCENE TO RECENT DIVERSITY OF CARIBBEAN BENTHIC FORAMINIFERA FROM THE CENTRAL AMERICAN ISTHMUS

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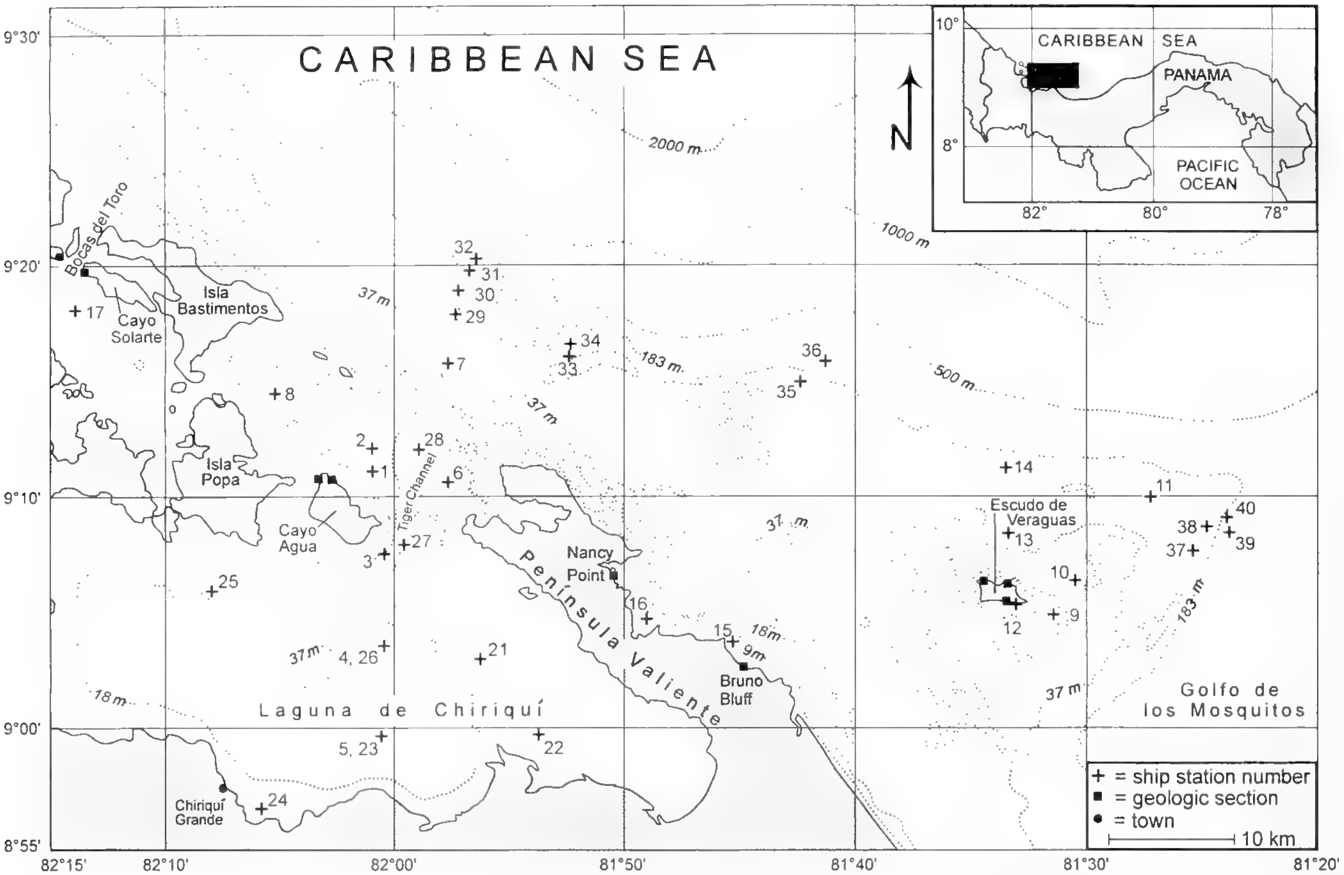
## INTRODUCTION

The diversity of modern benthic foraminifera in tropical America is lower in the Eastern Pacific than in the Caribbean. Culver and Buzas (1982, 1986, 1987) used all published literature on the coastal waters of North America to enumerate synonymized species: 1189 in the Caribbean, 798 from the Pacific coast between California and Baja, and 377 from the Mexican to Central American Pacific coast. Whereas the latter compilation by itself may suffer from inadequate sampling (Culver and Buzas, 1987), when it is combined with the Pacific California to Baja data set it is robust, as is the Caribbean one (Buzas and Culver, 1991). Diversity indices that take into account the relative abundance as well as the number of these same species further indicate that benthic foraminiferal diversity in the modern Caribbean is almost twice as high as in the tropical Eastern Pacific from Central America to California (Buzas and Culver, 1991). This pattern contrasts with those of most other invertebrate species: gastropod diversity is not demonstrably different in the Recent tropical Western Atlantic than in the Recent tropical Eastern Pacific (Allmon *et al.*, 1993), crustacean diversity does not appear appreciably different (Jones and Hasson, 1985), and echinoid diversity is approximately equal (Chesher, 1972). Only reef corals seem to have a similar Eastern Pacific-Caribbean contrast in the diversity of species: about 20 living in the East Pacific (Glynn, 1972) versus about 50 in the Caribbean (Johnson *et al.*, 1995), although species richness is substantially lower than for benthic foraminifera.

The historical reasons for differences in tropical Atlantic *vs.* Eastern Pacific diversity hinge on the evolutionary and biogeographic divergence of taxa caused by the closure of the Caribbean-Pacific seaway. Surface waters of the Caribbean and Pacific mixed before the isthmus emerged to constrict and close the seaway, so that assemblages were more similar and diversity lower before seaway closure than they are today. This is because the contrast in benthic foraminiferal diversity between the Caribbean and tropical Eastern Pacific almost certainly reflects oceanic conditions rather than the influence of biotic interactions (Buzas and Culver, 1998). Constriction of the seaway was advanced in Late Miocene time (Mikolajewicz *et al.*, 1993; Collins *et al.*, 1996a), and complete closure occurred approximately 3.5 Ma (Keigwin, 1982). Caribbean effects of the cutoff of Pacific waters should have been most pronounced closest to the seaway.

This study uses latest Middle Miocene to Recent benthic foraminifera from upper bathyal to inner neritic deposits of Caribbean Panama and Costa Rica to investigate the pattern of Caribbean diversity through the time of seaway constriction to closure. "Diversity" as used in this chapter refers to both the number of species and the distribution of individuals among species, *i.e.*, the relative abundances of the species (Peet, 1974). A fossil assemblage is comparable to a live + dead Recent assemblage. As the number of individuals in a community is counted, the number of species commonly increases.

Three hundred ninety-five species (Appendix 1), including undescribed ones (in some cases, preservation was too poor to distinguish between the two), were recognized in the 130 Miocene to Recent sediment samples of this study. There are probably another 50 species that I have not recognized in these assemblages because of their rarity and/or lack of good preservation of diagnostic features. All of the fossil species, from deposits of the Panama Canal Basin, the Bocas del Toro Basin, Panama, and the Limon Basin, Costa Rica (Coates, this volume), have been enumerated and form the basis of previous paleoenvironmental interpretations (Collins, 1993; Collins *et al.*, 1995, 1996b; Collins in Jackson *et al.*, this volume). Proportions of all common fossil species, defined herein as those represented by >1 specimen in a split of a sample collected by the Panama Paleontology Project (PPP), are presented in electronic form at the PPP internet site: http://www.fiu.edu/˜collinsl/. Abundances of the Recent taxa were listed by Havach and Collins (1997).



Text-figure 1.—Ship stations (+) for Recent foraminiferal assemblages, and land-based geologic sections (■) for fossil assemblages of the province of Bocas del Toro, northwestern Panama.

The diversity of a taxon such as benthic foraminifera or mollusks typically varies considerably across neritic depths, which effect or bias should be considered when examining biodiversity at this study's relatively small, regional scale. The ecological relationships of Recent foraminifera from 37 ship stations (Text-fig. 1), covering a wide range of habitats in the archipelago of Bocas del Toro, northwestern Panama (Havach and Collins, 1997), were applied to interpreting paleoenvironments of Costa Rica and Panama. In this study, the species proportions and diversity of the Recent and fossil assemblages are analyzed quantitatively and compared for similar environments. Because of generally strong associations of species with particular marine environments, the relatively long geologic ranges of species in this study (mean first occurrence of 21.4 Ma, similar to that in the U. S. Atlantic coastal plain calculated by Buzas and Culver, 1998), and the few Pliocene to Recent extinctions of Caribbean taxa common to these deposits (Collins, 1996), the expectation was that assemblages from the same environment, rather than age, would be most similar. Previous, smaller scaled studies of Miocene to Pliocene taxa of the Bocas del Toro and Limon basins (Collins *et al.*, 1995), and of Miocene taxa within the Panama Canal Basin (Collins *et al.*, 1996b), showed that paleoenvironment had a stronger influence than age on assemblage composition. This study combines all the basins and adds Pleistocene to Recent data in an evaluation of 130 late Middle Miocene to Recent Caribbean assemblages.

The main purpose of this chapter is to evaluate benthic foraminiferal diversity of the past 11 m.y. within similar marine environments of Caribbean Panama and Costa Rica. The chapter is divided into three parts: (1) a classification of the assemblages of fossil and Recent benthic foraminifera, using cluster analysis, to evaluate environmental and chronologic patterns. (2) an identification of the differences in diversity between Recent habitats/environments, using analyses of variance (ANOVAs), to apply as a yardstick in the paleobiodiversity study. (3) a study of diversity over time, taking into account the expected diversity differences between environments, to evaluate trends in relation to the Neogene closure of the Caribbean-Pacific seaway.

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## METHODS

### FIELD AND LABORATORY METHODS

Members of the Panama Paleontology Project (PPP) collected the geologic samples between 1986 and 1994. The PPP assigned each sampling site a PPP number (Appendix A, this volume), which is the main reference for all sediment samples and foraminiferal assemblages. I selected for preparation 50-g portions of ninety-three sediment samples (Table 1) from geologic sections (Appendix B, this volume) with biochronologic ages restricted to the shortest intervals of time. For all cases except the Gatun Formation, at least one sample within each geologic section was biochronologically dated. Gatun samples are from many small exposures measured over a wide area at the Caribbean end of the Panama Canal (Appendix A, Maps 1–2). For lower, middle and upper parts of the Gatun Formation, Panama Canal Basin, biochronologic indicators were either poorly preserved (calcareous nannoplankton) or sparse (planktic foraminifera) due to the shallowness of the paleoenvironment. Therefore, I transferred ages from dated portions to undated portions of the sections by correlating physical stratigraphic relationships among the sections.

For comparison with fossil material, I collected Recent marine sediment samples of 40 ml each from 3.7 to 240 m water depth in the Bocas del Toro archipelago (Text-fig. 1) using STRI's R/V *Benjamin*. Ship stations were chosen to maximize the estimated range of habitats in the area and to include habitats similar to those interpreted for the geologic samples. The categories of habitats covered were: lagoon, the main channel (Tiger Channel) between the lagoon and open ocean, nearshore, coral reef, open-ocean middle neritic, outer neritic, and upper bathyal. Havach and Collins (1997) described sampling and habitats in detail.

Fossil and Recent sediments were washed through a 63-μm sieve, which retains all adults and identifiable juveniles of benthic foraminifera. For samples in which foraminifera were exceedingly sparse (*e.g.*, the Bruno Bluff section, Shark Hole Point Formation), heavy-liquid separations of heavier grains from lighter foraminiferal tests were performed with sodium polytungstate. Each sample was split to yield $> 400$ benthic foraminifera, except for the few cases in which all washed residue yielded $< 400$ specimens. Four hundred is a sufficient number of individuals to accurately represent the proportional abundances of the species in the samples with a margin of error (confidence limits) of no more than ± 0.05 (Buzas, 1990). Specimens were sorted into species on cardboard micropaleontological slides, and species with $>1$ individual per sample were identified using comparative collections of specimens and the literature on Caribbean, Gulf of Mexico, and East Pacific Neogene to Recent benthic foraminifera. These methods for sample preparation are described in more detail by Collins (1993) and Havach and Collins (1997).

### METHODS OF NUMERICAL ANALYSES

The relationships among the assemblages of 395 recognized species were summarized by a Q-mode cluster analysis of relative abundances, which joins assemblages by their similarity of species proportions. I present results from Ward's method (Systat, 1998), in which the sum of the squares of the Euclidean distances was calculated between two clusters of assemblages added up over all the variables (taxa), and at each generation, the within-cluster sum of squares was minimized over all partitions obtainable by merging two clusters from the previous generation. Relative abundance data were transformed using the relationship $2 \arcsin \sqrt{P}$, where $P =$ the proportion of a species in an assemblage. Data were then standardized by the calculation of z values to approximate a multivariate normal distribution of the data matrix, which gives equal weight to all species in the calculation of the distances between assemblages.

Cluster analysis, an exploratory, classificatory method, was employed instead of more sophisticated, hypothesis-testing methods, such as discriminant analysis, because cluster analysis is one of the few methods in which the number of variables (species) can exceed the number of observations (assemblages). In tropical waters, the diversity of benthic foraminifera in a single cubic centimeter of washed, normal marine sediment

Table 1.—Paleobathymetry (range midpoints), ages (range midpoints) and diversity (α, Fisher's alpha) of benthic foraminiferal assemblages. The mean (μ), standard deviation (δ) and standard error of the mean ($\delta_\mu$), which is the average deviation of sample means from the expected value, are calculated for α in each stratigraphic unit or Recent habitat. Fossil assemblages are from the Panama Paleontology Project (PPP) and Recent assemblages are from Bocas del Toro (BDT) sites of Text-figure 1. * = environmental settings which are larger scaled than Recent habitats and used in Tables 2–6 and Text-figures 3–6.

| Stratigraphic unit or Recent habitat | Age (Ma) | Depth (m) | PPP or BDT No. | α | μ | δ | $\delta_\mu$ |
|---|---|---|---|---|---|---|---|
| **Fossil, PPP Collections** | | | | | | | |
| Lower Gatun Fm. | 11.6 | 25 | 6 | 11 | 13.0 | 7.2 | 2.5 |
| *Open Inner Neritic | | | 14 | 5 | | | |
| | | | 15 | 9 | | | |
| | | | 16 | 13 | | | |
| | | | 35 | 13 | | | |
| | | | 1037 | 29 | | | |
| | | | 1038 | 15 | | | |
| | | | 1040 | 9 | | | |
| Middle Gatun Fm. | 9.0 | 25 | 18 | 27 | 20.3 | 5.8 | 3.3 |
| *Open Inner Neritic | | | 19 | 17 | | | |
| | | | 34 | 17 | | | |
| Upper Gatun Fm. | 9.0 | 25 | 17 | 12 | 19.7 | 7.1 | 2.9 |
| *Open Inner Neritic | | | 20 | 23 | | | |
| | | | 27 | 15 | | | |
| | | | 28 | 18 | | | |
| | | | 160 | 32 | | | |
| | | | 1660 | 18 | | | |
| Chagres Fm., Rio Indio facies | 7.1 | 65 | 24 | 21 | 25.7 | 4.5 | 2.6 |
| *Middle Neritic | | | 26 | 30 | | | |
| | | | 1645 | 26 | | | |
| Chagres Fm. | 6.1 | 350 | 1088 | 22 | 19.5 | 3.7 | 1.9 |
| *Upper Bathyal | | | 1097 | 15 | | | |
| | | | 1173 | 18 | | | |
| | | | 1174 | 23 | | | |
| Nancy Point Fm. | 6.0 | 400 | 407 | 21 | 23.4 | 4.3 | 1.9 |
| *Upper Bathyal | | | 408 | 19 | | | |
| | | | 410 | 30 | | | |
| | | | 411 | 25 | | | |
| | | | 412 | 22 | | | |
| Shark Hole Point Fm., | 3.6 | 175 | 376 | 25 | 22.5 | 1.9 | 1.0 |
| Bruno Bluff section | | | 377 | 21 | | | |
| *Outer Neritic | | | 378 | 21 | | | |
| | | | 379 | 23 | | | |
| Cayo Agua Fm., NE section | 4.8 | 60 | 59 | 19 | 21.3 | 2.9 | 1.4 |
| *Middle Neritic | | | 60 | 22 | | | |
| | | | 61 | 19 | | | |
| | | | 62 | 25 | | | |
| Cayo Agua Fm., NW section | 3.6 | 30 | 57 | 23 | 17.8 | 3.7 | 1.5 |
| *Open Inner Neritic | | | 63 | 17 | | | |
| | | | 195 | 21 | | | |
| | | | 196 | 13 | | | |
| | | | 197 | 18 | | | |
| | | | 198 | 15 | | | |
| Cayo Solarte section | 3.6 | 50 | 68 | 21 | | | |
| *Middle Neritic | | | | | | | |
| Escudo de Veraguas Fm., SE | 3.6 | 125 | 168 | 41 | 43.3 | 4.0 | 2.3 |
| *Mixed M. Neritic & O. Neritic/U. Bathyal | | | 169 | 48 | | | |
| | | | 170 | 41 | | | |

Table 1.—Continued.

| Stratigraphic unit or Recent habitat | Age (Ma) | Depth (m) | PPP or BDT No. | α | μ | δ | $\delta_\mu$ |
|---|---|---|---|---|---|---|---|
| Escudo de Veraguas Fm., NE<br>*Mixed M. Neritic & O. Neritic/U. Bathyal | 3.6 | 125 | 365 | 34 | 39.2 | 5.4 | 2.4 |
| | | | 366 | 38 | | | |
| | | | 367 | 48 | | | |
| | | | 368 | 40 | | | |
| | | | 369 | 36 | | | |
| Escudo de Veraguas Fm., NW<br>*Mixed M. Neritic & O. Neritic/U. Bathyal | 1.8 | 125 | 358 | 48 | 39.2 | 7.6 | 3.4 |
| | | | 360 | 39 | | | |
| | | | 361 | 45 | | | |
| | | | 362 | 35 | | | |
| | | | 363 | 29 | | | |
| Swan Cay section<br>*Coral Reef | 1.4 | 100 | 1181 | 37 | 41.0 | 5.7 | 4.0 |
| | | | 1789 | 45 | | | |
| Uscari Fm., Carbon Dos section<br>*Upper Bathyal | 5.5 | 300 | 726 | 24 | 28.6 | 5.3 | 2.4 |
| | | | 727 | 27 | | | |
| | | | 728 | 32 | | | |
| | | | 729 | 36 | | | |
| | | | 730 | 24 | | | |
| Uscari Fm., Rio Sandbox section<br>*Upper Bathyal | 5.5 | 200 | 735 | 30 | 25.7 | 4.5 | 2.6 |
| | | | 736 | 26 | | | |
| | | | 737 | 21 | | | |
| Lower Rio Banano Fm.<br>*Open Inner Neritic | 3.6 | 30 | 679 | 43 | 32.4 | 8.4 | 3.8 |
| | | | 680 | 37 | | | |
| | | | 681 | 21 | | | |
| | | | 682 | 28 | | | |
| | | | 683 | 33 | | | |
| Upper Rio Banano Fm.<br>*Open Inner Neritic | 2.5 | 20 | 668 | 31 | 29.3 | 4.3 | 1.8 |
| | | | 669 | 28 | | | |
| | | | 670 | 29 | | | |
| | | | 671 | 26 | | | |
| | | | 677 | 37 | | | |
| | | | 678 | 25 | | | |
| Moin Fm., type section<br>*Mixed M. Neritic & O. Neritic/U. Bathyal | 1.8 | 200 | 647 | 41 | 32.4 | 10.3 | 3.0 |
| | | | 648 | 21 | | | |
| | | | 649 | 27 | | | |
| | | | 650 | 38 | | | |
| | | | 651 | 25 | | | |
| | | | 652 | 57 | | | |
| | | | 653 | 25 | | | |
| | | | 654 | 40 | | | |
| | | | 655 | 32 | | | |
| | | | 656 | 32 | | | |
| | | | 657 | 22 | | | |
| | | | 658 | 29 | | | |
| Moin Fm., Lomas del Mar section<br>*Coral Reef | 1.8 | 75 | 638 | 60 | 37.3 | 18.8 | 9.4 |
| | | | 640 | 28 | | | |
| | | | 641 | 17 | | | |
| | | | 642 | 44 | | | |
| **Recent, BDT Collections** | | | | | | | |
| Recent, shallow lagoon<br>*Lagoon | 0 | 18 | 21A | 23 | 19.8 | 8.3 | 4.2 |
| | | 12 | 22A | 14 | | | |
| | | 14 | 24A | 12 | | | |
| | | 14 | 25A | 30 | | | |
| Recent, deep lagoon<br>*Lagoon | 0 | 21 | 4C | 24 | 27.8 | 3.9 | 1.9 |
| | | 34 | 5A | 28 | | | |
| | | 35 | 23A | 26 | | | |
| | | 25 | 26A | 33 | | | |

Table 1.—Continued.

| Stratigraphic unit or Recent habitat | Age (Ma) | Depth (m) | PPP or BDT No. | α | μ | δ | $\delta_\mu$ |
|---|---|---|---|---|---|---|---|
| Recent, channel | 0 | 34 | 1B | 37 | 37.0 | 11.1 | 5.0 |
| *Middle Neritic | | 33 | 2A | 33 | | | |
| | | 27 | 3B | 44 | | | |
| | | 70 | 27A | 50 | | | |
| | | 45 | 28A | 21 | | | |
| Recent, nearshore | 0 | 24 | 8A | 29 | 36.5 | 5.4 | 2.7 |
| *Open Inner Neritic | | 6 | 15B | 36 | | | |
| | | 15 | 16A | 5 | | | |
| | | 11 | 17A | 40 | | | |
| Recent, inner middle neritic | 0 | 39 | 6C | 22 | 24.5 | 3.5 | 2.5 |
| *Middle Neritic | | 56 | 7B | 27 | | | |
| Recent, outer middle neritic | 0 | 73 | 29A | 50 | 48.0 | 2.8 | 2.0 |
| *Middle Neritic | | 80 | 33A | 46 | | | |
| Recent, coral reef | 0 | 18 | 9B | 41 | 36.5 | 11.2 | 4.6 |
| *Coral Reef | | 35 | 10B | 30 | | | |
| | | 64 | 11C | 39 | | | |
| | | 4 | 12B | 46 | | | |
| | | 49 | 13A | 46 | | | |
| | | 82 | 14C | 17 | | | |
| Recent, outer neritic | 0 | 120 | 30A | 40 | 37.0 | 2.5 | 1.2 |
| *Outer Neritic | | 168 | 31C | 35 | | | |
| | | 120 | 34C | 38 | | | |
| | | 180 | 35A | 35 | | | |
| Recent, upper bathyal | 0 | 230 | 32A | 32 | 32.5 | 0.7 | 0.5 |
| *Upper Bathyal | | 235 | 36A | 33 | | | |
| Recent, outer neritic/upper bathyal | 0 | 113 | 37A | 55 | 67.3 | 12.1 | 6.1 |
| mixed with middle neritic | | 164 | 38A | 65 | | | |
| *Mixed M. Neritic & O. Neritic/U. | | 203 | 39A | 65 | | | |
| Bathyal | | 240 | 40B | 84 | | | |

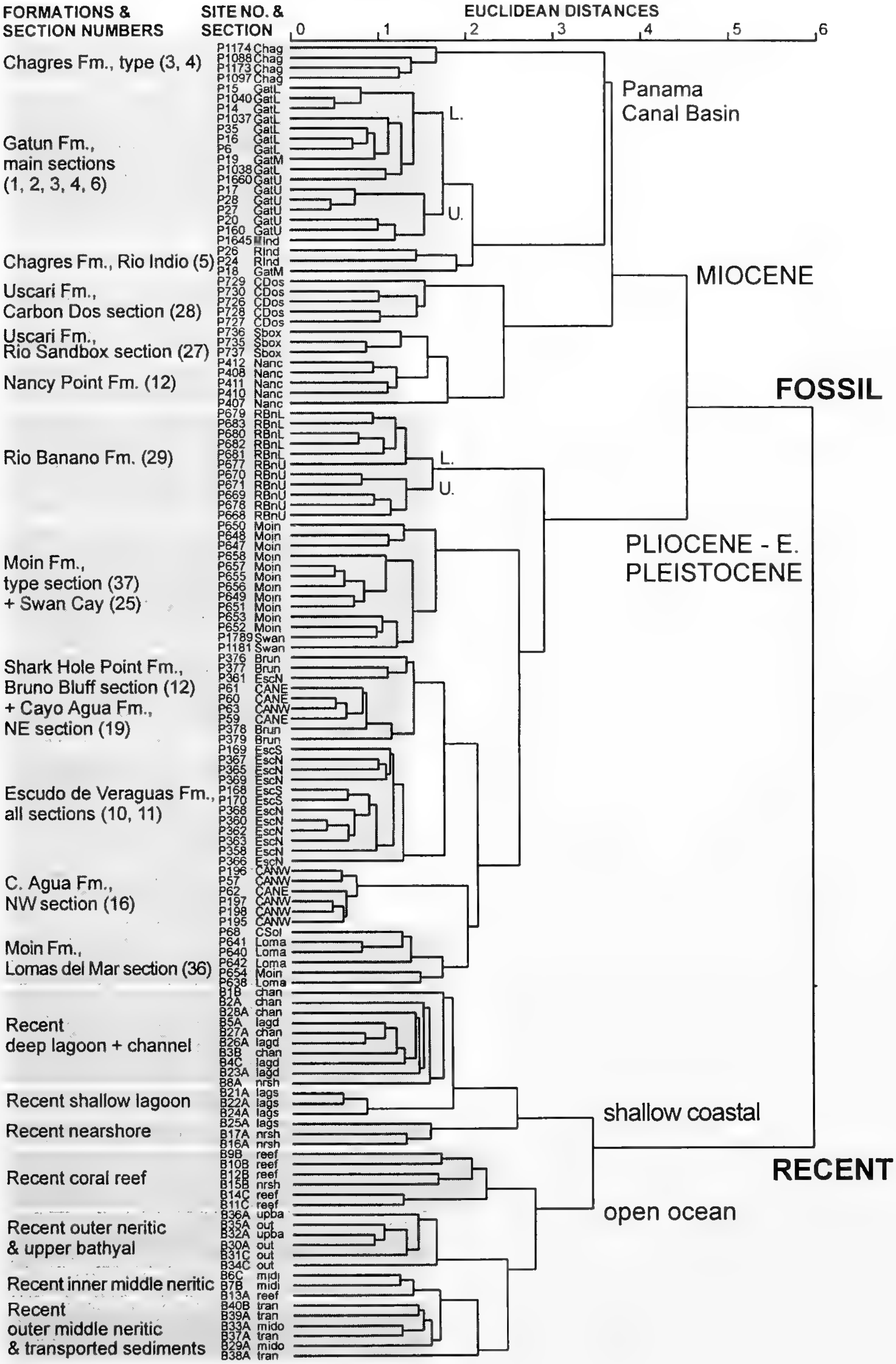
is commonly > 100. Reducing the number of species to less than the number of assemblages in a data set that covers such a large range of time and space would be too great a loss of information to assess relationships among the assemblages. Conversely, increasing the number of assemblages to more than the number of species, even if few additional ones were recovered, is impracticable.

The diversity of foraminiferal assemblages was measured for Recent habitats and for sections of geologic formations with Fisher's alpha (α), an index which assumes that the proportions of species within assemblages are distributed in a log series. This distribution has successfully predicted the frequency of benthic foraminiferal species occurrences from the North American Atlantic coast, Gulf of Mexico and the Caribbean (Buzas *et al.*, 1982). Calculations for α use the number of taxa and the number of specimens; iterative solutions for α for combinations of these parameters were obtained from Hayek and Buzas (1997, Appendix 4).

Analyses of variance (ANOVAs) were performed on diversity data and relative abundances and proportions of carbonate-associated taxa to test relationships among mean values for different environments or time intervals, entities that were defined *a priori*. Analysis of variance tests whether the variances of the means among the groups are greater than expected on the basis of the variances within the groups. An F-test quantifies the significance of the overall differences

→

Text-figure 2.—Cluster analysis (Wards algorithm) of assemblages (rows) grouped by similarity of standardized species abundances. Fossil sites are referenced by PPP numbers ('P' prefix). Recent sites are referenced by BDT numbers ('B' prefix). Section numbers in left column refer to the stratigraphic sections of Appendix B (this volume). Assemblages cluster primarily by formation sections (shaded), which cluster by epoch (Miocene, Pliocene to Pleistocene, or Recent) before depositional environment.


FORMATIONS & SECTION NUMBERS
SITE NO. & SECTION
EUCLIDEAN DISTANCES
0
1
2
3
4
5
6
Chagres Fm., type (3, 4)
Gatun Fm., main sections (1, 2, 3, 4, 6)
Chagres Fm., Rio Indio (5)
Uscari Fm., Carbon Dos section (28)
Uscari Fm., Rio Sandbox section (27)
Nancy Point Fm. (12)
Rio Banano Fm. (29)
Moin Fm., type section (37) + Swan Cay (25)
Shark Hole Point Fm., Bruno Bluff section (12) + Cayo Agua Fm., NE section (19)
Escudo de Veraguas Fm., all sections (10, 11)
C. Agua Fm., NW section (16)
Moin Fm., Lomas del Mar section (36)
Recent deep lagoon + channel
Recent shallow lagoon
Recent nearshore
Recent coral reef
Recent outer neritic & upper bathyal
Recent inner middle neritic
Recent outer middle neritic & transported sediments
P1174 Chag
P1088 Chag
P1173 Chag
P1097 Chag
P15 GatL
P1040 GatL
P14 GatL
P1037 GatL
P35 GatL
P16 GatL
P6 GatL
P19 GatM
P1038 GatL
P1660 GatU
P17 GatU
P28 GatU
P27 GatU
P20 GatU
P160 GatU
P1645 RInd
P26 RInd
P24 RInd
P18 GatM
P729 CDos
P730 CDos
P726 CDos
P728 CDos
P727 CDos
P736 Sbox
P735 Sbox
P737 Sbox
P412 Nanc
P408 Nanc
P411 Nanc
P410 Nanc
P407 Nanc
P679 RBnL
P683 RBnL
P680 RBnL
P682 RBnL
P681 RBnL
P677 RBnU
P670 RBnU
P671 RBnU
P669 RBnU
P678 RBnU
P668 RBnU
P650 Moin
P648 Moin
P647 Moin
P658 Moin
P657 Moin
P655 Moin
P656 Moin
P649 Moin
P651 Moin
P653 Moin
P652 Moin
P1789 Swan
P1181 Swan
P376 Brun
P377 Brun
P361 EscN
P61 CANE
P60 CANE
P63 CANW
P59 CANE
P378 Brun
P379 Brun
P169 EscS
P367 EscN
P365 EscN
P369 EscN
P168 EscS
P170 EscS
P368 EscN
P360 EscN
P362 EscN
P363 EscN
P358 EscN
P366 EscN
P196 CANW
P57 CANW
P62 CANE
P197 CANW
P198 CANW
P195 CANW
P68 CSol
P641 Loma
P640 Loma
P642 Loma
P654 Moin
P638 Loma
B1B chan
B2A chan
B28A chan
B5A lagd
B27A chan
B26A lagd
B3B chan
B4C lagd
B23A lagd
B8A nrsh
B21A lags
B22A lags
B24A lags
B25A lags
B17A nrsh
B16A nrsh
B9B reef
B10B reef
B12B reef
B15B nrsh
B14C reef
B11C reef
B36A upba
B35A out
B32A upba
B30A out
B31C out
B34C out
B6C midi
B7B midi
B13A reef
B40B tran
B39A tran
B33A mido
B37A tran
B29A mido
B38A tran
L.
U.
Panama Canal Basin
MIOCENE
FOSSIL
L.
U.
PLIOCENE - E. PLEISTOCENE
shallow coastal
RECENT
open ocean

among the groups to test whether the group means are different because of differences in the underlying population means. In this study, if the probability that the means of the groups were drawn from the same population is low ($P < 0.05$), the groups of environments or time intervals were considered significantly different.

## SIMILARITY OF LATE MIOCENE TO RECENT ASSEMBLAGES

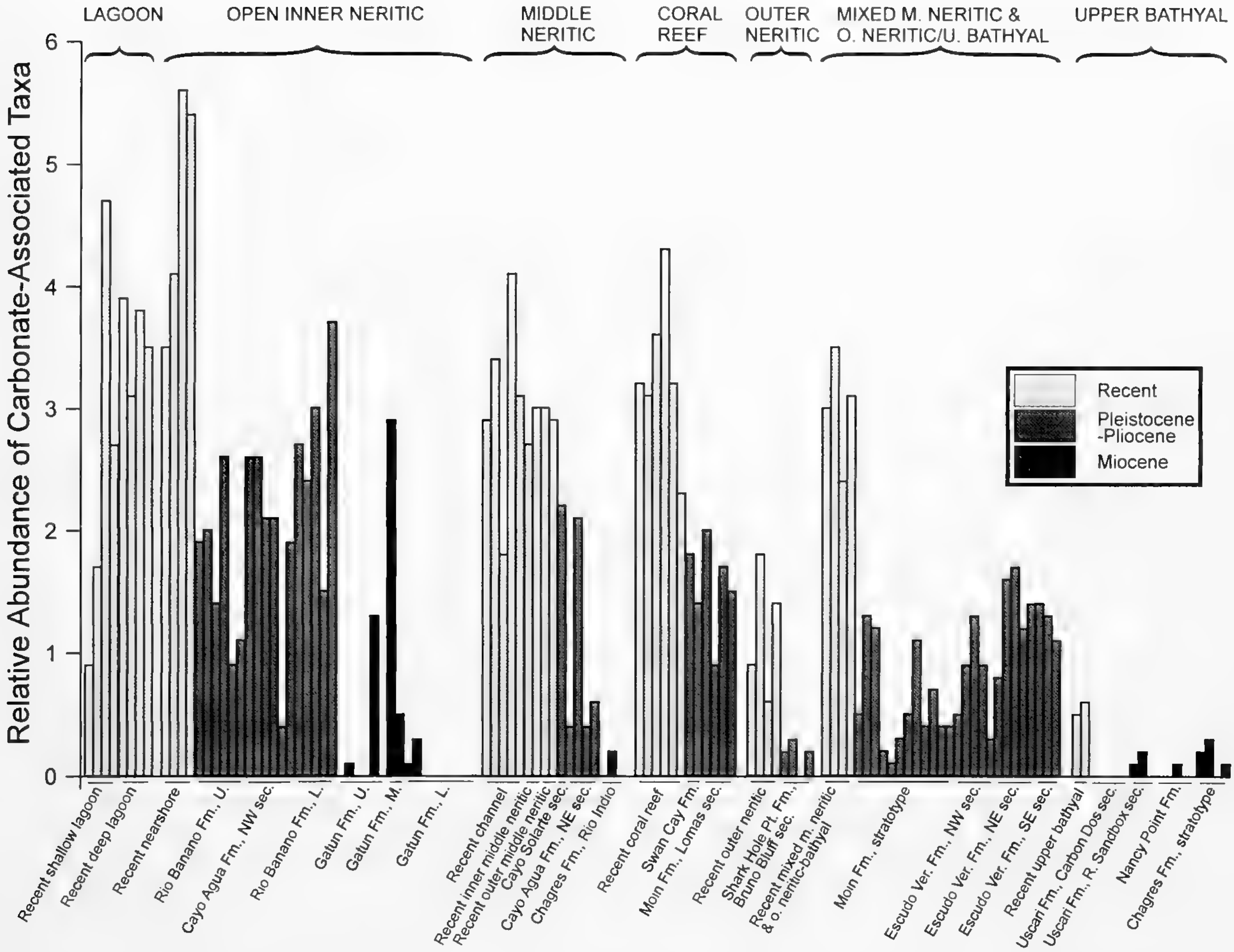
Age (epoch), rather than environment, has a stronger influence on the similarity of the 130 Miocene to Recent benthic foraminiferal assemblages. A cluster analysis (Text-fig. 2) shows the principal division on the right between fossil and Recent assemblages, and secondarily within fossil assemblages between the Miocene and Pliocene to Early Pleistocene (~1.4 Ma). These results differ from those of several previous, smaller scale cluster analyses in which isthmian benthic foraminiferal assemblages from different ages but similar environments were the most similar. Cluster analyses were previously performed on assemblages from the Late Miocene to Late Pliocene of the Bocas del Toro Basin (32 samples; Collins, 1993), the Late Miocene to Late Pliocene of the Bocas del Toro and Limon basins (67 samples; Collins *et al.*, 1995), and the late Middle to Late Miocene of the Panama Canal Basin (9 samples; Collins *et al.*, 1996b). In these earlier analyses, clusters were joined by paleobathymetry rather than age. However, in the present study, ages span a longer time interval (late Middle Miocene to Recent) but not a greater bathymetric range (although the Recent data include a new, distinctive lagoonal environment). Extending the ages analyzed downward to the late Middle Miocene (Lower Gatun Formation) and upward to the Recent (of Bocas del Toro) clearly increases the disparity among assemblages more than adding additional depositional environments.

Assemblages cluster by age despite an overlap in comparable modern and fossil environments, based on ecologic relationships of environment-diagnostic, extant taxa (Collins *et al.*, 1995, 1996b). For example, environments of the Late Miocene Gatun Formation (~25 m deep), the Early Pliocene Cayo Agua Formation (~20–40 m deep), the Late Pliocene Rio Banano Formation (upper part ~20 m and lower part ~20–40 m deep), and the modern nearshore, middle neritic, and lagoon habitats are all characterized by similar depth ranges with many of the same species, but their assemblages cluster according to the three ages. Similarly, outer neritic to uppermost bathyal sediments that are mixed with shallower, reefal and siliciclastic-associated species, such as those of the Late Pliocene type Moin and Escudo de Veraguas formations and Recent ship stations 38 to 40, are separated on the basis of age. Coral-reef-associated species of the latest Pliocene Lomas del Mar (paleodepth ~75 m) and Early Pleistocene Swan Cay (paleodepth ~100 m) sections are within the same age cluster but not grouped most closely. The four Early Pleistocene assemblages are more similar to those of the Late Pliocene than Recent, despite the wide range of water depths sampled off living coral reefs of the island of Escudo de Veraguas (Text-fig. 1). In the Panama Canal Basin, most Gatun Formation species are inner neritic and of Caribbean affiliation, whereas the Chagres Formation species are of Pacific affiliation and upper bathyal (Collins *et al.*, 1996b), two very different paleoenvironments. However, they cluster together when compared with Pliocene to Recent assemblages.

Assemblages from the same formation sections or Recent habitats form coherent groups that represent discrete subenvironments. This cluster analysis supports previous results that show the closest relationships (Text-fig. 2, on the left) to be within formation sections for fossil material (Collins, 1993; Collins *et al.*, 1995, 1996b) and within habitats or groups of similar habitats for Recent material (Havach and Collins, 1997). Only 12% of the assemblages were classified outside of their sections or habitats.

The cluster dendrogram (Text-fig. 2) was produced with the Wards algorithm, only one of several methods available. Other explored methods (average, single, centroid, median and complete linkage) yielded few clusters and "stringy" dendrograms, mostly joining assemblages one at a time to preceding ones. Similarity is more interpretable from clusters rather than strings, so Wards method, which is among the best available (Milligan, 1980), was preferred. In general, the few groupings of some Recent and fossil assemblages produced by the other methods, such as a few lagoon to middle neritic Recent and Rio Banano Formation assemblages (complete linkage algorithm), offer little insight into paleoenvironmental or other interpretations.

How do Miocene, Pliocene to Early Pleistocene, and Recent assemblages differ in composition? Most of the Miocene assemblages, from the Uscari, Nancy Point and Chagres formations, are from deeper (bathyal) biofacies than the Recent samples (~240 m deep), and most of the common Chagres species are Pacific. (Collins *et al.*, 1996b, explain this anomalous Caribbean occurrence with a breached isthmus.) The Miocene type Gatun Formation (inner neritic) and the Rio Indio facies (middle neritic) of the Chagres Formation mostly contain species associated with siliciclastic sediments with low abundances of carbonate-associated species, unlike the other neritic assemblages.



Text-figure 3.—Relative abundances of taxa primarily associated with carbonate shoals and reefs, plotted for the 130 assemblages. Assemblages are grouped by sections of formations (fossil) or marine habitat (Recent), as in the cluster analysis, then ordered by the marine environments across the top. Within comparable environments, Recent assemblages include the most carbonate-associated taxa, Pliocene to Early Pleistocene the next highest, and Miocene the least (see Table 2 for means.)

Table 2.—Mean relative abundances of taxa that are generally associated with carbonate facies (Miliolina and larger foraminifera) for the groupings by age and environment of Text-figure 3. Within environments, values increase over time.

| | Recent | Pliocene to Pleistocene | Miocene |
|---|---|---|---|
| Lagoon | 3.0 | | |
| Inner Neritic | 4.7 | 2.1 | 0.3 |
| Middle Neritic | 3.0 | 1.1 | 0.1 |
| Coral Reef | 3.3 | 1.6 | |
| Outer Neritic | 1.2 | 0.2 | |
| Mixed M. Neritic & O. Neritic/U. Bathyal | 3.0 | 0.9 | |
| Upper Bathyal | 0.6 | | 0.06 |

An important age-related trend in the composition of assemblages is an increase in individuals and species associated with carbonate shoals and coral reefs. These carbonate-associated species are primarily of the suborder Miliolina (those with calcareous, imperforate tests) and, to a much lesser extent, larger foraminifera (those having morphologically complex, calcareous, perforate chambers and sizes larger than most benthic foraminifera). Their mean relative abundance (Text-fig. 3, Table 2) and proportions of total taxa at the neritic to bathyal depths show significant increases within different environments over the three age intervals (Table 3, ANOVAs). Of 98 Recent species that are not represented as fossils, about one-fourth are Miliolina and larger foraminifera, mostly the former. If 39 rare species (they occur in only one sample) are excluded to reduce potential sampling biases, and 3

Table 3.—ANOVA tables, mean relative abundances (left column) and proportions (right column) of Miliolina and larger foraminifera (Text-fig. 3). All ANOVAs indicate overall significant differences among the three age categories (Miocene, Pliocene to Early Pleistocene, and Recent) within different environments, except for proportions of taxa in the reef environment (P = 0.0563).

| RELATIVE ABUNDANCE | | | | | | PROPORTION OF SPECIES | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Source of variability | df | Sum of squares | Mean square | F | p(F) | Source of variability | df | Sum of squares | Mean square | F | p(F) |
| OPEN INNER NERITIC | | | | | | | | | | | |
| Age | 2 | 66.61 | 33.30 | 49.53 | 0.0000 | Age | 2 | 7264.23 | 3632.11 | 47.23 | 0.0000 |
| Error | 34 | 22.86 | 0.67 | | | Error | 35 | 2691.58 | 76.90 | | |
| MIDDLE NERITIC | | | | | | | | | | | |
| Age | 2 | 23.63 | 11.81 | 25.89 | 0.0000 | Age | 2 | 4167.91 | 2083.96 | 48.95 | 0.0000 |
| Error | 14 | 6.39 | 0.46 | | | Error | 14 | 596.09 | 42.58 | | |
| CORAL REEF | | | | | | | | | | | |
| Age | 1 | 9.01 | 9.01 | 31.26 | 0.0002 | Age | 1 | 533.33 | 533.33 | 4.66 | 0.0563 |
| Error | 10 | 2.88 | 0.29 | | | Error | 10 | 1145.33 | 114.53 | | |
| OUTER NERITIC | | | | | | | | | | | |
| Age | 1 | 2.00 | 2.00 | 13.41 | 0.0106 | Age | 1 | 840.50 | 840.50 | 160.1 | 0.0000 |
| Error | 6 | 0.90 | 0.15 | | | Error | 6 | 31.50 | 5.25 | | |
| MIXED MIDDLE NERITIC & OUTER NERITIC/UPPER BATHYAL | | | | | | | | | | | |
| Age | 1 | 15.79 | 15.79 | 70.13 | 0.0000 | Age | 1 | 1365.55 | 1365.55 | 17.37 | 0.0003 |
| Error | 27 | 6.08 | 0.23 | | | Error | 27 | 2123.00 | 78.63 | | |
| UPPER BATHYAL | | | | | | | | | | | |
| Age | 1 | 0.43 | 0.43 | 50.21 | 0.0000 | Age | 1 | 215.37 | 215.37 | 75.13 | 0.0000 |
| Error | 17 | 0.15 | 0.01 | | | Error | 17 | 48.74 | 2.87 | | |

species are excluded because they are fragile (delicate agglutinated or thin-walled calcareous), to reduce potential preservational biases, about half (30) of the remaining 56 species are in the Miliolina or larger foraminifera. This is an approximation, as not all of the Miliolina are primarily carbonate-associated (*e.g., Sigmoilina tenuis* is in most assemblages) and some hyaline foraminifera (*e.g., Neoeponides repandus*) or agglutinated species (*e.g., Bigenerina irregularis*) that are carbonate-associated are not included in this count. However, the relatively large proportion of Miliolina plus larger foraminifera that appears in the Recent assemblages suggests that carbonate-associated taxa have increased substantially in Caribbean isthmian waters during Pleistocene to Recent time.

## DIVERSITY IN RECENT HABITATS OF BOCAS DEL TORO

Differences in diversity due to differences in environments should be taken into account when analyzing changes in diversity through time if environments have also changed. In this study, paleoenvironments of the Caribbean side of the Central American isthmus have varied in paleobathymetry from upper bathyal to inner neritic. They also vary from predominantly siliciclastic to carbonate sediments produced *in situ* by coral reefs (Collins *et al.*, 1995, 1996b). Based on general bathymetric subdivisions, as well as the results of a previous study (Havach and Collins, 1997), the Recent assemblages are assigned *a priori* to the following seven environments: lagoon, open-ocean inner neritic, middle neritic, coral reef, outer neritic, mixed middle to outer neritic/uppermost bathyal, and upper bathyal. These divisions were also distinguished by the paleoenvironmental studies based on benthic foraminifera. The "mixed " assemblages, *i.e.*, those that contain many taxa transported from middle neritic depths, have artificially high values of diversity because they combine shallower, middle neritic and deeper, outer neritic or uppermost bathyal (~240 m deep) species. The interpretation of mixed assemblages is also supported by clearly middle neritic values of stable isotopes of oxygen from the benthic foraminiferal tests (Havach and Collins, 1997). The isotopic signals do not reflect a "mixed" signal because the species analyzed, *Cibicides pachyderma,* lives predominantly at middle neritic depths.

Analyses of variance were performed to identify significant differences in diversity among the seven bathymetric divisions. The first ANOVA (Table 4, top) indicates an overall, significant difference in diversity among environments ($P < 0.00005$), but dropping out the anomalously high mixed middle to outer neritic/uppermost bathyal group (with an almost doubled apparent biodiversity) reduces differences among environment means to insignificant levels (Table 4, bottom).

Table 4.—ANOVA tables, mean diversity ($\alpha$) of Recent environments of Text-figure 4. The top table indicates significant differences in diversity among environments (lagoon, open-ocean inner neritic, middle neritic, reef, outer neritic, outer neritic/uppermost bathyal with transported sediments, and uppermost bathyal). However, this is due to the artificially high values for the assemblages that include transported middle neritic sediments. If these are excluded (bottom table), average diversity among the other environments is not significantly different.

All 7 Environments

| Source of variability | df | Sum of squares | Mean square | F | p(F) |
|---|---|---|---|---|---|
| Environment | 6 | 5108.64 | 851.44 | 9.74 | 0.0000 |
| Error | 30 | 2623.25 | 87.44 | | |

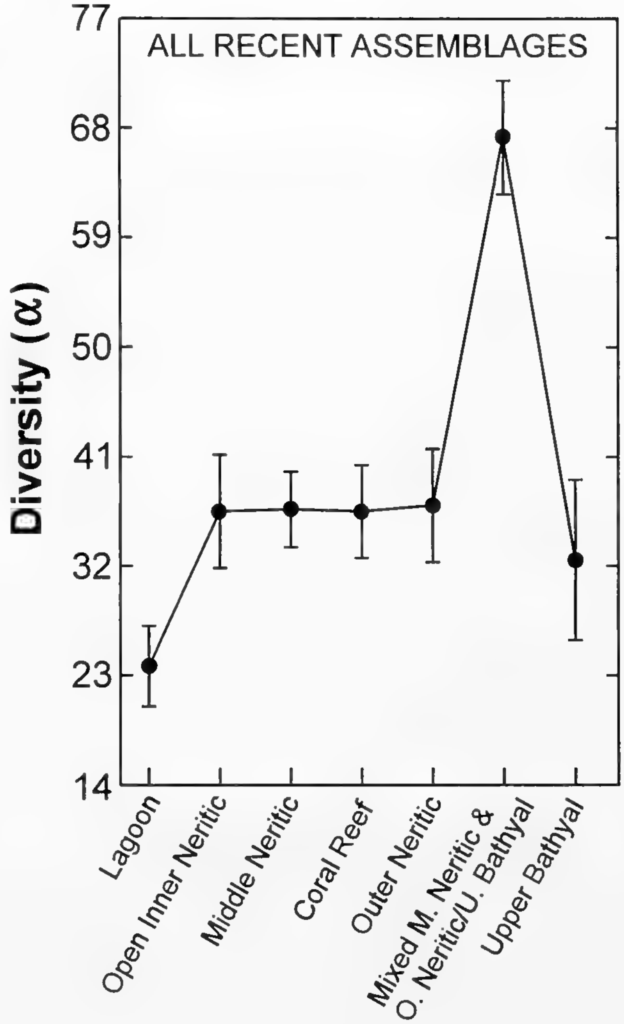
Excluding Mixed M. Neritic & O. Neritic/U. Bathyal

| Source of variability | df | Sum of squares | Mean square | F | p(F) |
|---|---|---|---|---|---|
| Environment | 5 | 990.05 | 198.01 | 2.45 | 0.0592 |
| Error | 27 | 2182.50 | 80.83 | | |

Excluding the "mixed" group, the main differences are for the lagoonal assemblages, which have the lowest diversity, and the upper bathyal assemblages, which have a lower diversity than open-ocean neritic assemblages (Text-fig. 4). Not only are the differences among the open neritic groups insignificant, including open inner neritic, middle neritic, reef, and outer neritic, but the mean $\alpha$s for these environments are also quite similar, all falling between 36 and 37. The similarity of open-ocean neritic diversities is surprising because previous studies, based in areas of cooler waters, show that benthic foraminiferal species diversity increases from the shoreline to shelf edge (summarized by Sen Gupta, 1982), so that the pattern in this study may be a Caribbean or warm-water phenomenon. In applying the results to the fossil data below, the following should be noted: (1) A lagoonal facies is not represented in the paleoenvironments analyzed for this study. (2) The open-ocean inner neritic, middle neritic, coral reef, and outer neritic environments are analyzed together as well as separately. (3) The upper bathyal assemblages are analyzed separately.

## LATE MIOCENE TO RECENT BIODIVERSITY

On the basis of the similar diversity of benthic foraminifera among subdivisions of Recent, open-ocean neritic depths (open inner neritic, middle neritic, coral reef, and outer neritic), the diversities of fossil and Recent assemblages were analyzed together in an ANOVA with age (Miocene, Pliocene to Early Pleistocene, or Recent) as the classification criterion. Twenty-five assemblages from the type section of the Moin and Escudo de Veraguas formations were excluded because they contain greatly varying amounts of downshelf to downslope transport of shallower taxa, so diversity values are influenced primarily by sedimentary processes rather than true biodiversity. The environments represented by the type Moin and Escudo de Veraguas formations are similar to the Recent "mixed assemblages" containing many shallow-water, coral-reef-associated species that mixed with typical outer neritic to upper bathyal species. In fact, the sections of the Moin Formation form a relict Pliocene relief. The type Moin section is located at the base of a steep hill composed largely of in-place hermatypic corals (Lomas del Mar section, Moin Formation). Both sections are latest Pliocene, and many of the benthic fo-



Text-figure 4.—For Recent environments, least squares means of diversity ($\alpha$) and their standard deviation (error bars) predicted by the ANOVA of Table 4 (top). The data suggest that diversity does not differ significantly among environments of Bocas del Toro, and the most similar are open-ocean inner neritic, middle neritic, coral reef and outer neritic depths. The high value is an artefact of mixing assemblages from different environments and does not reflect true biodiversity.

Table 5.—ANOVA table, mean diversity (α) of open-ocean, inner to outer neritic assemblages for Miocene, Pliocene to Early Pleistocene, and Recent ages (plotted in Text-fig. 5). Outer neritic assemblages of the type Moin and Escudo de Veraguas formations have been excluded because the varying proportions of downshelf-transported taxa result in unreliable estimates of biodiversity.

| | | Open Inner to Outer Neritic | | | |
|---|---|---|---|---|---|
| Source of variability | df | Sum of squares | Mean square | F | p(F) |
| Age | 2 | 3731.45 | 1865.73 | 21.52 | 0.0000 |
| Error | 72 | 6241.22 | 86.68 | | |

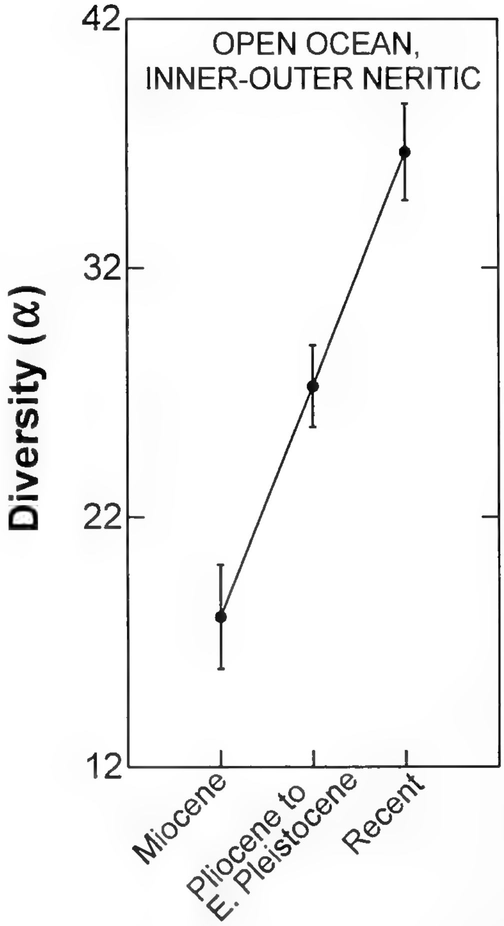
raminiferal species which I collected (1989) between fronds of Pliocene corals are also found at the base of the slope in the type Moin deposits.

Overall, average neritic diversity for Miocene, Pliocene to Early Pleistocene, and Recent ages are significantly different ($P < 0.00005$; Table 5). Text-figure 5 shows a large increase from a mean of 18 in the Late Miocene ($N = 20$, which includes the open inner neritic to outer middle neritic Gatun Formation and Rio Indio biofacies of the Chagres Formation), to a mean of 27 in the Pliocene to Early Pleistocene ($N = 32$, which includes the open inner neritic, middle neritic, coral reef and outer neritic environments of the Swan Cay Formation, Lomas del Mar section of the Moin Formation, Rio Banano Formation, Cayo Agua Formation, and Cayo Solarte section), to a mean of 35 in the Recent ($N = 23$, which includes open inner neritic, middle neritic, coral reef, and outer neritic). The data indicate that the diversity of Caribbean benthic foraminifera from neritic depths along the Central American isthmus increased from Late Miocene to the Recent.

Within-environment ANOVAs would be useful to examine patterns at a scale smaller than the entire open-ocean neritic interval (Table 5, Text-fig. 5). However, data are too few for meaningful analysis of most of the environmental divisions, except perhaps for open inner neritic and upper bathyal (Table 6, Text-fig. 6). Where statistically significant, within-environment ANOVA results do support the pattern of increasing diversity (α) over time with no reversals, as follows:

1. Open Inner Neritic. For $N_{\text{Miocene}} = 17$, $N_{\text{Pliocene}} = 17$, $N_{\text{Recent}} = 4$, age differences are significant and show increasing diversity with time (Table 6, top; Text-fig. 6, left).

2. Middle Neritic. Data are too few ($N_{\text{Miocene}} = 3$, $N_{\text{Pliocene}} = 5$, $N_{\text{Recent}} = 9$) for convincing results (not shown), although overall they are significant ($P = 0.0202$). An ANOVA indicates that Miocene and Pliocene values of alpha are not significantly different (standard deviations from the least squares means

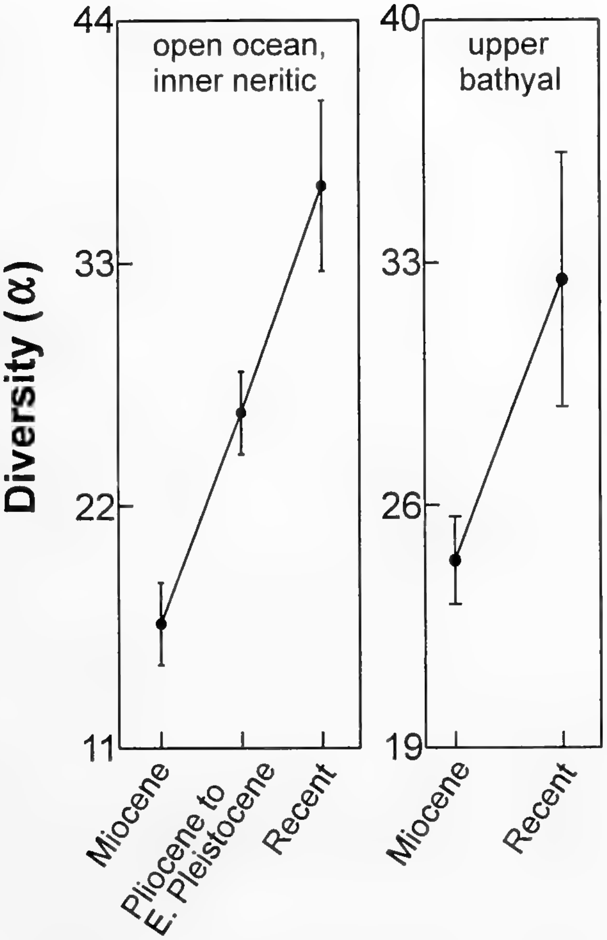


Text-figure 5.—For Recent and fossil, open-ocean, inner to outer neritic environments (the four divisions are inner, middle, coral reef, outer), least squares means of diversity (α) and their standard error (bars) predicted by the ANOVA of Table 5. The data suggest that open-ocean, neritic diversity in the isthmian region increased from the Late Miocene to Recent.

Table 6.—ANOVA tables, mean diversity (α) of open-ocean inner neritic and upper bathyal environments for Miocene, Pliocene to Early Pleistocene, and Recent ages (plotted in Text-fig. 6). These environments have sufficient data to test within-group differences per age. The data suggest that diversity has increased in these Caribbean isthmian environments since the Miocene.

| | | Open Inner Neritic | | | |
|---|---|---|---|---|---|
| Source of variability | df | Sum of squares | Mean square | F | p(F) |
| Age | 2 | 1586.65 | 793.32 | 13.33 | 0.0000 |
| Error | 35 | 2083.35 | 59.52 | | |

| | | Upper Bathyal | | | |
|---|---|---|---|---|---|
| Source of variability | df | Sum of squares | Mean square | F | p(F) |
| Age | 1 | 117.07 | 117.07 | 4.32 | 0.0531 |
| Error | 17 | 460.62 | 27.10 | | |



Text-figure 6.—For inner neritic and upper bathyal environments, least squares means of diversity (α) and their standard error (bars) predicted by the ANOVAs of Table 6. The data suggest that diversity within these groups has increased in the isthmian region since the Miocene.

overlap), but diversity shows a statistically significant increase from the Pliocene to Recent.

3. Coral Reef. For the few data ($N_{\text{late Pliocene-Pleistocene}} = 6$, $N_{\text{Recent}} = 6$), standard deviations from the least squares means overlap and there is a high probability ($P = 0.7981$) that means are not significantly different. Alpha has a higher variability for Coral Reef relative to other environments. The diversity of benthic foraminiferal reef assemblages is very high when species from nearby reefs are mixed with siliciclastically associated taxa (*e.g.*, BDT13A, $\alpha = 46$), but α is low, with several dominant taxa (*e.g.*, BDT14C, $\alpha = 17$), when sediments are coarse, well winnowed sand.

4. Outer Neritic. Data are too few ($N_{\text{Pliocene}} = 4$, $N_{\text{Recent}} = 4$) for convincing results (not shown), but there is a significant increase in diversity with age ($P = 0.0001$).

5. Upper Bathyal. For $N_{\text{Miocene}} = 17$ and $N_{\text{Recent}} = 2$, age differences are significant and show higher diversity in the Recent than in the Miocene (Table 6, bottom; Text-fig. 6, right).

## CONCLUSIONS

This study investigates Miocene to Recent diversity in Caribbean benthic foraminifera of the Central American isthmus for the time interval spanning the constriction to complete closure of the Pacific-Caribbean seaway. The seaway was constricted in the Late Miocene and completely closed by middle Pliocene time, ~3.5 Ma. Because the seaway was located in southern Central America to northwestern Colombia, the effects of its closure should have been most pronounced in this region.

Benthic foraminiferal diversity in the Caribbean sedimentary basins of Panama and Costa Rica doubled from the Miocene to Recent, through the time of seaway constriction, complete closure, and afterward. Fisher's alpha (α), a diversity index that takes into account the number of species and the distribution of individuals among those species, shows significant increases within the neritic biota as a whole, as well as within the bathymetric divisions of neritic to upper bathyal. For the neritic biota as a whole, $\alpha = 18$ for the Late Miocene, 27 for the Pliocene to Early Pleistocene, and 37 for the Recent.

The largest differences in the composition of benthic foraminiferal assemblages, as shown by cluster analysis, are also among the analyzed intervals of Late Miocene, Pliocene to Early Pleistocene, and Recent, rather than among the fairly disparate inner neritic to upper bathyal environments. A great difference among the three time intervals is the relative abundance of specimens and proportion of species associated with carbonate reefs and shoals. This trend reflects the Late Miocene to Pliocene evolutionary pattern of increasing speciation in common, carbonate-associated taxa in the Caribbean (Collins, 1996; Collins *et al.*, 1996a; Pleistocene to Recent speciation was not examined). This pattern and other supporting data suggested that oceanographic changes caused by the closing seaway resulted in increasing carbonate content and accelerated origination of carbonate-associated taxa. The present study indicates that the trend of increasing diversity in carbonate-associated taxa from Miocene to Pliocene time continued until the present, well after complete seaway closure.

If seaway closure had the greatest effect on the composition and diversity of isthmian benthic foraminiferal assemblages, the largest biogeographic and evolutionary responses should have occurred during and/or soon afterward. However, the largest faunal changes apparently occurred in the Pleistocene to Recent interval. Recent asssemblages are the most different from Late Miocene and Early Pleistocene assemblages according to cluster analysis, and a large proportion (one-fourth, or 98) of the isthmian species occur only in the Recent assemblages. This pattern holds even if 39 rare and fragile species, those most likely to bias comparisons of fossil and Recent assemblages, are excluded. Few Late Miocene to Recent extinctions occurred in isthmian benthic foraminifera. Thus, although the diversity increase from the Miocene to Pliocene was approximately the same as from the Pliocene to Recent, the greatest change in assemblage composition occurred during the Pleistocene to Recent, 2–4 m.y. after complete seaway closure, as a result of speciation and/or migration.

There are few other studies of Neogene changes in the diversity of benthic foraminiferal species, but a recent analysis of 356 neritic, Paleocene to Pliocene species of North Carolina, Virginia and Maryland by Buzas and Culver (1998) shows a similar trend. In that study, diversity (Fisher's alpha, sample values combined per time interval) increased from 15 in the Early to Middle Miocene to 20 in the Early and Late Pliocene, with a decrease to 7 in the Late Miocene (possibly due to a cooling interval). The general pattern of a Miocene to Pliocene increase is similar to the Caribbean results and is also due in part to a low extinction rate, although Caribbean diversity ($\alpha$ values per sample, not equivalent to the combined sample values) increased more rapidly, from 18 to 27. It is unknown whether the difference in rates of increase between the temperate and tropical Western Atlantic faunas was due to temperature differences (diversity is generally higher at lower latitudes), to the addition of more carbonate-rich taxa in the Caribbean than in the temperate Northwestern Atlantic, or to a stronger effect of seaway closure on benthic foraminifera closer to the Central American isthmus, including an hypothesized North Atlantic warming caused by the emergence of the isthmus (Berger and Wefer, 1996).

Changes in the Caribbean diversity of Neogene benthic foraminifera at first paralleled those of reef corals and possibly mollusks from the Late Miocene to Pliocene, but then diverged. The Neogene diversity of Caribbean mollusks (Jackson *et al.*, 1993, this volume; genera to subgenera) either increased or remained steady.That of reef corals (Johnson *et al.*, 1995; species) increased from Late Miocene to Pliocene time. Whereas benthic foraminiferal diversity continued to increase to the Recent with few extinctions (Collins, 1996), mollusks and reef corals experienced Late Pliocene to Pleistocene turnovers, perhaps because of glacial cooling intervals, and coral diversity decreased significantly from the Late Pliocene to Recent (Johnson *et al.*, 1995). There are no comparable molluscan data for Neogene *versus* Recent diversity. However, in terms of species richness, the Late Pliocene (378) is similar to the Recent (390; Jackson *et al.*, 1993), suggesting that a diversity increase may not have continued until the present.

Only data from the Caribbean side of the Central American isthmus are analyzed herein, so a relative diversity pattern across the isthmus is, at present, undetermined. Research in progress on Pacific Neogene benthic foraminifera of Darien, Panama (Collins *et al.*, 1998) and coastal Ecuador is producing assemblage information comparable to the Caribbean data to more fully address the fundamental question of the effect of a biogeographic barrier, the Isthmus of Panama, on marine diversity.

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## APPENDIX 1
## Benthic Foraminiferal Species

Listed below are the 395 fossil and Recent species that are used in this study. Not included are taxa identified to only the genus level, which are a minor component of the assemblages. The data set of the distribution of taxa among samples is archived at the PPP internet web site, located at http://www.fiu.edu/˜collinsl/.

*Alabamina decorata*
*Ammobaculoides* sp. a
*Ammonia beccarii*
*Amphicoryna sublineata*
*Amphistegina gibbosa*
*Anomalina* sp. b
*Archaias angulatus*
*Articulina mayori*
*Articulina pacifica*
*Articulina sagra*
*Articulina* sp. a
*Asterigerina carinata*
*Asterigerina pettersi*
*Asterigerinata dominicana*
*Astrononion* sp. a
*Bigenerina irregularis*
*Biloculinella eburnea*
*Bolivina alata*
(includes var. *pseudobeyrichii*)
*Bolivina albatrossi*
*Bolivina barbata*
*Bolivina byramensis*
*Bolivina caudriae*
*Bolivina churchi*
*Bolivina floridana*
*Bolivina fragilis*
*Bolivina goesii*
*Bolivina imporcata*
*Bolivina inflata*
*Bolivina isidroensis*
*Bolivina ligularia*
*Bolivina lowmani*
*Bolivina marginata*
*Bolivina merecuanai*
*Bolivina multicostata*
*Bolivina paula*
*Bolivina pisciformis*
*Bolivina plicatella*
*Bolivina pozonensis*
*Bolivina pseudoplicata*
*Bolivina simplex*
*Bolivina* sp. 1
*Bolivina* sp. 2
*Bolivina* sp. a
*Bolivina* sp. b
*Bolivina* sp. c
*Bolivina* sp. d
*Bolivina* sp. e
*Bolivina* sp. f
*Bolivina* sp. g
*Bolivina* sp. h
*Bolivina* sp. i
*Bolivina striatula*
*Bolivina subaenariensis*
*Bolivina subaenariensis mexicana*
*Bolivina subexcavata*
*Bolivina subspinescens*
*Bolivina subspinescens zanzibarica*
*Bolivina tectiformis*
*Bolivina tongi*
*Bolivina tongi filacostata*
*Bolivina tortuosa*
*Bolivina translucens*
*Bolivina vaughani*
*Bronnimannia palmerae*
*Buccella hannai*
*Bulimina aculeata*
*Bulimina affinis*
*Bulimina falconensis*
*Bulimina marginata*
*Bulimina* sp.a
*Bulimina striata mexicana*
*Bulimina tessellata*
*Buliminella curta*
*Buliminella elegantissima*
*Buliminoides milletti*
*Buliminoides williamsonianus*
*Cancris sagra*
*Cassidulina bradyi*
*Cassidulina carapitana*
*Cassidulina corbyi*
*Cassidulina crassa*
*Cassidulina laevigata*
*Cassidulina minuta*
*Cassidulina norcrossi australis*
*Cassidulina* sp. a
*Cassidulina* sp. b
*Cassidulina* sp. x
*Cassidulina subglobosa*
*Cassidulina tortuosa*
*Cassidulinoides compacta*
*Cassidulinoides* sp. 1
*Chilostomella ovoidea*
*Cibicides colombianus*
*Cibicides compressus*
*Cibicides culebrensis*
*Cibicides floridanus*
*Cibicides lobatulus*
*Cibicides matanzasensis*
*Cibicides pachyderma*
*Cibicides protuberans*
*Cibicides* sp. a
*Cibicides* sp. b
*Cibicidina* sp. a
*Clavulina carinata*
*Clavulina communis*
*Clavulina nodosaria*
*Clavulina tricarinata*
*Compressigerina coartata*
*Cornuspira planorbis*
*Cycloputeolina discoideus*
*Cycloputeolina pseudodiscoidea*
*Cymbaloporetta atlantica*
*Cymbaloporetta bradyi*
*Cymbaloporetta squamosa*
*Dentalina advena*
*Discorbina patelliformis*
*Discorbinella minuta*
*Discorbis bulbosa*
*Discorbis helicoidalis*
*Discorbis mira*
*Discorbis* sp. c
*Dorothia* sp. a
*Dyocibicides biserialis*
*Eggerella advena*
*Ehrenbergina falcata*
*Ehrenbergina* sp. 1
*Ehrenbergina* sp. a
*Elphidium excavatum*
*Elphidium fimbriatulum*
*Elphidium gunteri*
*Elphidium hispidulum*
*Elphidium lanieri*
*Elphidium mexicanum*
*Elphidium poeyanum*
*Elphidium* sp. a
*Elphidium translucens*
*Eoeponidella delicatula*
*Epistominella exigua*
*Epistominella* sp. a
*Epistominella vitrea*
*Eponides* sp. a
*Fischerina helix*
*Fischerina* sp. a
*Fissurina ampullacea*
*Fissurina circularis*
*Fissurina crebra*
*Fissurina diaphana*
*Fissurina laevigata*
*Fissurina marginata*
*Fissurina orbignyana*
*Fissurina* aff. *F. orbignyana*
*Fissurina pseudoglobosa*
*Fissurina striolata*
*Fursenkoina complanata*
*Fursenkoina mexicana*
*Fursenkoina pontoni*
*Fursenkoina* sp. a
*Fursenkoina spinicostata*
*Gaudryina aequa*
*Gaudryina exilis*
Genus 1 sp. 1
*Glabratella mirabilis*
*Glabratella* sp. a
*Glandulina glans*
*Glandulina laevigata*
*Globobulimina affinis*
*Guttulina kishinouyi*
*Guttulina problema*
*Gyroidina praecinctus*
*Gyroidina regularis*
*Gyroidina soldanii altiformis*
*Gyroidina* sp. a
*Gyroidina* sp. b
*Gyroidina* sp. c
*Gyroidina turgida*
*Gyroidina umbonata*
*Hanzawaia* aff. *H. concentrica*
*Hanzawaia concentrica*
*Hanzawaia isidroensa*
*Hanzawaia* sp. a
*Haplophragmoides* sp. a
*Hauerina bradyi*
*Hauerina fragilissima*
*Hauerina* sp. a
*Haynesina depressula*

*Haynesina germanica*
*Haynesina* sp. a
*Haynesina* sp. b
*Heronallenia lingulata*
*Heterillina cribrostoma*
*Heterostegina antillarum*
*Heterostegina depressa*
*Hoeglundina elegans*
*Hopkinsina glabra*
*Laevipeneroplis proteus/carinatus*
*Lagena semistriata*
*Lagena amphora*
*Lagena clavata*
*Lagena hispidula*
*Lagena montagui*
*Lagena ornata*
*Lagena striata*
*Lagena substriata*
*Lagena vulgaris*
*Lagenammina atlantica*
*Lamarckina atlantica*
*Lenticulina calcar*
*Lenticulina clericii*
*Lenticulina peregrina*
*Lenticulina* sp. a
*Lenticulina* sp. b
*Marginulina glabra*
*Marginulina triangularis*
*Marginulinopsis marginulinoides*
*Marginulinopsis* sp. a
*Massilina protea*
*Melonis barleeanum*
*Melonis* sp. a
*Miliolinella californica*
*Miliolinella dilatata*
*Miliolinella fichteliana*
*Miliolinella oblonga*
*Miliolinella* sp. a
*Miliolinella* sp. b
*Miliolinella* sp. c
*Miliolinella* sp. d
*Mychostomina revertens*
*Neoconorbina alveata*
*Neoconorbina frustata*
*Neoconorbina parkerae*
*Neoconorbina terquemi*
*Neoeponides antillarum*
*Neoeponides repandus*
*Nodobaculariella cassis*
*Nodosaria longiscata*
*Nodosaria pyrula*
*Nodosaria* sp. a
*Nonion inflatiformis*
*Nonion* sp. a
*Nonion* sp. b
*Nonionella atlantica*
*Nonionella basiloba*
*Nonionella grateloupi*
*Nonionella incisa*
*Nonionella labradorica*
*Nonionella miocenica*
*Nonionella obducta*
*Nonionella soldadoensis*
*Nonionella* sp. a
*Nonionella* sp. b
*Nonionella* sp. c
*Nonionella turgida*
*Nubecularia lucifuga*
*Oolina melo*
*Opthalmidium concava*
*Opthalmidium* sp. a
*Oridorsalis umbonatus*
*Parafissurina dorbignyana*
*Parafissurina subcircularis*
*Pararotalia magdalenensis*
*Pararotalia rosea*
*Parasorites orbitolitoides*
*Patellina corrugata*
*Peneroplis bradyi*
*Peneroplis carinatus*
*Peneroplis pertusus*
*Peneroplis proteus*
*Planogypsina squamiformis*
*Planorbulina mediterranensis*
*Planorbulinella larvata*
*Planulina ariminensis*
*Planulina charapotoensa*
*Planulina exorna*
*Planulina foveolata*
*Planulina* sp. 1
*Plectofrondicularia californica*
*Pullenia bulloides*
*Pullenia quinqueloba*
*Pyrgo nasutus*
*Pyrgo oblonga*
*Pyrgo* sp. a
*Pyrgo subsphaerica*
*Quinqueloculina agglutinans*
*Quinqueloculina berthelotiana*
*Quinqueloculina bicornis*
*Quinqueloculina bicostata*
*Quinqueloculina candeiana*
*Quinqueloculina collumnosa*
*Quinqueloculina compta*
*Quinqueloculina costata*
*Quinqueloculina cuvieri*
*Quinqueloculina funafutiensis*
*Quinqueloculina goesi*
*Quinqueloculina gracilis*
*Quinqueloculina horrida*
*Quinqueloculina impressa*
*Quinqueloculina lamarckiana*
*Quinqueloculina parkeri*
*Quinqueloculina poeyana*
*Quinqueloculina seminula*
*Quinqueloculina* sp. 1
*Quinqueloculina* sp. a
*Quinqueloculina* sp. b
*Quinqueloculina* sp. d
*Quinqueloculina* sp. e
*Quinqueloculina* sp. f
*Quinqueloculina* sp. g
*Quinqueloculina* sp. i
*Quinqueloculina* sp. j
*Quinqueloculina* sp. k
*Quinqueloculina* sp. l
*Quinqueloculina* sp. m
*Quinqueloculina* sp. n
*Quinqueloculina tricarinata*
*Rectobolivina advena*
*Rectobolivina glabra*
*Rectobolivina limbata*
*Rectobolivina* sp. a
*Reophax scorpiurus*
*Reussella minuta*
*Reussella spinulosa*
*Rosalina candeiana*
*Rosalina concinna*
*Rosalina floridana*
*Rosalina floridensis*
*Rosalina globularis*
*Rosalina* sp. a
*Rosalina subaraucana*
*Rotalia garveyensis*
*Rotorbinella umbonata*
*Sagrina pulchella*
*Sagrina* sp. a
*Sahulia conica*
*Saracenaria* sp. a
*Saracenaria vaughani*
*Scutuloris* sp. a
*Seabrookia earlandii*
*Sigmavirgulina tortuosa*
*Sigmoilina tenuis*
*Sigmoilopsis schlumbergeri*
*Siphogenerina lamellata*
*Siphonaperta* sp. a
*Siphonides* sp. a
*Siphonina pulchra*
*Siphoninella soluta*
*Sorites marginalis*
*Sphaeroidina bulloides*
*Spirillina vivipara*
*Spiroloculina antillarum*
*Spiroloculina depressa*
*Spiroloculina hancocki*
*Spiroloculina ornata*
*Spiroloculina* sp. a
*Spiroplectammina floridana*
*Stetsonia minuta*
*Stilostomella antillea*
*Stilostomella verneuili*
*Subedentostomina lavelaenus*
*Svratkina tubulifera*
*Textularia conica*
*Textularia foliacea occidentalis*
*Textularia lalickeri*
*Textularia leuzingeri*
*Textularia panamensis*
*Textularia schencki*
*Textularia sica*
*Textularia* sp. a
*Tiphotrocha comprimata*
*Trifarina bradyi*
*Trifarina carinata*
*Trifarina cojimarensis*
*Trifarina eximia*
*Trifarina occidentalis*
*Trifarina* sp. 1
*Trifarina* sp. a
*Triloculina fitterei*
*Triloculina* sp. a
*Triloculina* sp. b
*Triloculina* sp. c
*Triloculina trigonula*
*Trochammina advena*
*Trochammina comprimata*
*Tubinella funalis*
*Uvigerina canariensis*
*Uvigerina laevis*
*Uvigerina peregrina*
*Uvigerina* sp. a
*Valvulineria haitiana*
*Valvulineria palmerae*
*Valvulineria* sp. a
*Valvulineria* sp. b
*Valvulineria* sp. c
*Vulvulina miocenica*
*Wiesnerella auriculata*

# CHAPTER 6

## STRATIGRAPHIC DISTRIBUTION OF NEOGENE CARIBBEAN AZOOXANTHELLATE CORALS (SCLERACTINIA AND STYLASTERIDAE)

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### INTRODUCTION

This paper presents occurrence data and analyses of the azooxanthellate Caribbean Scleractinia, and, together with the paper of Budd *et al.* (1994), provides a listing of all known Caribbean Scleractinia from the Miocene to Recent. Whereas the zooxanthellate coral compilation was based almost exclusively on previously reported fossil faunas (Budd *et al.*, 1994: Table 2), this paper is based not only on historical collections (Table 1), but also on extensive new material from the Pliocene of Panama and Costa Rica.

Azooxanthellate corals are sometimes incorrectly referred to as "deep-water", "solitary", or "ahermatypic" (non-reef) corals. Whereas a majority of azooxanthellate corals do occur in water deeper than 200 m, the depth range of this ecological class of corals is intertidal to 6328 m. Because their distribution is not limited by the light requirement of algal symbionts (zooxanthellae), they not only occur below the euphotic zone, but also at temperatures of −1° to 29° and at latitudes ranging from the Arctic Circle to continental Antarctica (Cairns and Stanley, 1982). A majority of azooxanthellate coral genera are solitary in growth form, but one-third of the Recent genera are colonial, some colonies even forming extensive deep-water (to 1300 m) banks, and one azooxanthellate species, *Tubastraea micranthus,* forming shallow-water hermatypic reefs (Zibrowius, 1989). From the point of view of biodiversity, there is currently an equal number of Recent azooxanthellate and zooxanthellate scleractinian genera (*i.e.,* 114 of each) and approximately 620 valid Recent azooxanthellate species, compared to a range of 640–833 valid Recent zooxanthellate scleractinian species (Veron, 1995). Numbers of fossil species have not been tabulated. Therefore, although azooxanthellate corals are usually small and inconspicuous, they are widespread in the marine environment and have a biodiversity equal to their zooxanthellate ecological counterparts.

### ACKNOWLEDGMENTS

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### MATERIAL AND METHODS

The new specimens mentioned above were collected during the first seven years of the Panama Paleontology Project (PPP) 1986–1992. Descriptions of the lithostratigraphy and biostratigraphic correlations of the PPP region were given by Coates *et al.* (1992), Collins (1993) and Collins *et al.* (1995), as well as being summarized in this volume (Coates). The PPP corals are listed in Table 2, the new species and stratigraphic range extensions having been reported by Cairns (1995). Absolute dates for many of the PPP collecting sites were derived from biostratigraphic dating using planktic foraminifera, calcareous nannoplankton, and the Neogene time scale of Berggren *et al.* (1985). Ages for previously collected Neogene corals were derived from the original publications (Table 1), Budd *et al.* (1994: Table 3), and Cairns and Wells (1987).

In the analyses of taxonomic turnover rates, species and generic richnesses were calculated using the "range through method", wherein a species is assumed to be present during all time intervals between its earliest and latest occurrences, even if it was not found in all intermediate intervals. In the paleoecological analysis, the method of inferring the depth range of a formation from which a coral assemblage was collected was done in the following manner. The reported bathymetric ranges of the species with both fossil and Recent occurrences (Table 3) were combined with those of living species believed to be closely related as determined by morphological similarity (*i.e.,* Recent counterparts) to others fossil species found in a formation, *e.g.,* Cayo Agua Formation, which in this example results in a range of 1–653 m. Therefore, because most of the species used as bathymetric indica-

Table 1.—Distribution and stratigraphic range of Caribbean Neogene Azooxanthellate Scleractinia and Stylasteridae. Localities: A, Costa Rica; B, Panama; C, Colombia; D, Venezuela; E, Trinidad; F, Carriacou; G, Martinique; H, Dominican Republic; I, Jamaica.

| | Localities | | | | | | | | | Stratigraphic range |
|---|---|---|---|---|---|---|---|---|---|---|
| | A | B | C | D | E | F | G | H | I | |
| ANTHOZOA | | | | | | | | | | |
| **Fungiacyathidae** | | | | | | | | | | |
| 1 *Fungiacyathus* sp. cf. **F. symmetricus* sensu Wells, 1971 | | | | | | 10 | | | | late Early Miocene |
| **Rhizangiidae** | | | | | | | | | | |
| 2 *Septastraea marylandica* (Conrad, 1841) | | X | | | | | | | | M. Miocene–Pleistocene |
| =*S. matsoni* Vaughan, 1919 | | | 4 | | | | | | | |
| 3 *Septastraea altispina* Cairns, 1995 | | X | | | | | | | | early Late Pliocene |
| 4 **Phyllangia americana* Milne Edwards & Haime, 1849 | | | | 9 | | | | | | E. Pliocene–Recent |
| **Oculinidae** | | | | | | | | | | |
| 5 *Archohelia limonensis* Vaughan, 1919 | X | | | | | | | | | early Late–Late Pliocene |
| **Caryophylliidae** | | | | | | | | | | |
| 6 *Caryophyllia communis* sensu Wells, 1971 | | | | | | 10 | | | | early M. Miocene |
| 7 *Caryophyllia* sp. cf. **C. antillarum* sensu Wells, 1971 | | | | | | 10 | | | | late Early–early M. Miocene |
| 8 *Antillocyathus maoensis* (Vaughan, 1925) | | | | | | | | 6 | | Late Miocene–Early Pliocene |
| 9 *Antillocyathus alatus* Cairns & Wells, 1987 | | | | | | | | 12 | | Late Miocene–Early Pliocene |
| 10 *Antillocyathus cristatus* (Vaughan, 1925) | X | X | | | | | | 6 | | Late Miocene–Late Pliocene |
| 11 *Antillocyathus gracilis* Cairns, 1995 | | X | | | | | | | | early Late Pliocene |
| 12 *Trochocyathus chevalieri* Cairns & Wells, 1987 | X | X | | | | | | 12 | | Late Miocene–Late Pliocene |
| 13 *Trochocyathus duncani* Cairns & Wells, 1987 | | | | | | | | 12 | | Early Pliocene |
| 14 *Trochocyathus* sp. cf. **T. rawsonii* sensu Wells, 1971 | | | | | | 10 | | | | late Early Miocene |
| 15 *Ceratotrochus* cf. *duodecimcostatus* (Goldfuss, 1826) | | | | | | | | 2 | | Late Miocene |
| 16 *Paracyathus henekeni* (Duncan, 1863) | | X | | | | | | 1 | | ?M. Miocene–early L. Pliocene |
| 17 *Paracyathus sinuosus* Cairns & Wells, 1987 | | | | | | | | 12 | | Late Miocene–early L. Pliocene |
| 18 *Paracyathus adetos* Cairns, 1995 | | X | | | | | | | | early Late Pliocene |
| 19 **Paracyathus pulchellus* (Philippi, 1842) | | | | 9 | | | | | | Early Pliocene–Recent |
| 20 *Oxysmilia pliocenica* Cairns, 1995 | | X | | | | | | | | early Late Pliocene |
| 21 **Deltocyathus italicus* (Michelotti, 1838) | | | | | | | | 5 | | M. Miocene–Recent |
| 22 *Deltocyathus* sp. sensu Wells, 1971 | | | | | | 10 | | | | early M. Miocene |
| 23 *Stephanocyathus* sp. sensu Wells, 1971 | | | | | | 10 | | | | early M. Miocene |
| 24 *Asterosmilia abnormalis* (Duncan, 1864) | | | | | | | | 2 | | L. Miocene–Early Pliocene |
| 25 *Asterosmilia exarata* Duncan, 1867 | | X | | | | | | 3 | | L. Miocene–Late Pliocene |
| =*A. hilli* Vaughan, 1919 | 4 | | | | | | | | 4 | |
| 26 *Asterosmilia profunda* (Duncan, 1864) | X | X | | | | | | 5 | 2 | L. Miocene–L. Pliocene |
| 27 *Asterosmilia duncani* Vaughan, 1925 | | | | | | | | 6 | | Early Miocene |
| 28 *Asterosmilia compressa* Vaughan, 1925 | | | | | | | | 6 | | Early Miocene |
| 29 *Asterosmilia irregularis* Cairns, 1995 | X | | | | | | | | | Late Pliocene |
| 30 *Asterosmilia trinitatis* Vaughan in Vaughan & Hoffmeister, 1926 | | | | | 7 | | | | | Early Miocene |
| 31 *Asterosmilia machapooriensis* Vaughan in Vaughan & Hoffmeister, 1926 | | | | | 7 | | | | | Early Miocene |
| 32 *Desmophyllum* sp. sensu Wells, 1971 | | | | | | 10 | | | | early M. Miocene |

Table 1.—Continued.

| | Localities | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | A | B | C | D | E | F | G | H | I | Stratigraphic range |
| **Turbinoliidae** | | | | | | | | | | |
| 33 *Dominicotrochus dominicensis* (Vaughan, 1925) | | | | | | | 8 | 6 | | M. Miocene |
| 34 *Sphenotrochus senni* Wells, 1945 | | | | | | | 8 | 12 | 8 | M. Miocene–L. Pliocene |
| 35 *Sphenotrochus trinitatis* Vaughan in Vaughan & Hoffmeister, 1926 | | | | | 7 | | | | | Early Miocene |
| 36 *Sphenotrochus brassensis* Vaughan in Vaughan & Hoffmeister, 1926 | | | | | 7 | | | | | L. Miocene–Early Pliocene |
| 37 *Sphenotrochus* cf. *hancocki* Durham & Barnard, 1952 | 11 | X | | | | | | | | early L. Pliocene–L. Pliocene |
| **Flabellidae** | | | | | | | | | | |
| 38 *Flabellum* sp. sensu Vaughan & Woodring, 1921 | | | | | | | | 5 | | Late Miocene |
| 39 *Flabellum* sp. 1 sensu Wells, 1971 | | | | | | 10 | | | | early M. Miocene |
| 40 *Flabellum* sp. 2 sensu Wells, 1971 | | | | | | 10 | | | | early M. Miocene |
| 41 **Gardineria minor* Wells, 1973a | X | | | | | | | | | Late Pliocene–Recent |
| **Guyniidae** | | | | | | | | | | |
| 42 **Guynia annulata* Duncan, 1872 | X | X | | | | | | 12 | | Early Pliocene–Recent |
| 43 *Stenocyathus* sp. sensu Wells, 1971 | | | | | | 10 | | | | late Early Miocene |
| 44 **Schizocyathus fissilis* Pourtalès, 1874 | | X | | | | | | | | Late Pliocene–Recent |
| 45 **Pourtalocyathus hispidus* (Pourtalès, 1878) | | | | | | | | 12 | | Late Miocene–Recent |
| **Dendrophylliidae** | | | | | | | | | | |
| 46 *Balanophyllia pittieri* Vaughan, 1919 =?**B. grandis* Cairns, 1977 | 4 | X | | | | | | | | early L. Pliocene–L. Pliocene (Recent) |
| 47 *Balanophyllia* sp. sensu Wells, 1971 | | | | | | 10 | | | | late Early Miocene–early M. Miocene |
| 48 **Dendrophyllia cornucopia* Pourtalès, 1871 | | | | | | | | 12 | | Late Miocene–Recent |
| 49 *Dendrophyllia* sp. sensu Wells, 1971 | | | | | | 10 | | | | late Early Miocene |
| HYDROZOA | | | | | | | | | | |
| **Stylasteridae** | | | | | | | | | | |
| 50 **Stylaster roseus* (Pallas, 1766) | X | X | | | | | | | | early L. Pliocene–Recent |
| | 11 | 15 | 1 | 2 | 4 | 12 | 2 | 20 | 3 | |

1 Duncan, 1863; 2 Duncan, 1864; 3 Duncan, 1867; 4 Vaughan, 1919; 5 Vaughan and Woodring, 1921; 6 Vaughan and Hoffmeister, 1925; 7 Vaughan and Hoffmeister, 1926; 8 Wells, 1945; 9 Weisbord, 1968; 10 Wells, 1971; 11 Wells, 1983; 12 Cairns and Wells, 1987.

X New records reported herein (Table 2) from Caribbean coast of Panama and Costa Rica.

* Species also known from the Recent; L = Late; M = Middle.

Table 2.—Occurrences of azooxanthellate corals in PPP samples (numbered across top). Data are at the PPP internet site, http://www.fiu.edu/~collinsl/.

| | 53 | 55 | 56 | 57 | 63 | 65 | 66 | 168 | 170 | 177 | 178 | 179 | 180 | 189 | 193 | 194 | 195 | 196 | 197 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Septastraea altispina* | | | | | | | | | | | | | | | | | x | x | |
| *Septastraea marylandica* | | | | | | | | | | | | | | | | | | | |
| *Antillocyathus gracilis* | | x | x | x | x | | | | | | | | | | x | x | | x | x |
| *Antillocyathus cristatus* | | | | | | | | | | | | | | | | | | | |
| *Trochocyathus chevalieri* | | | | | | | | | | | | x | | | | | | | |
| *Paracyathus henekeni* | | | | | | | | | | | | | | | | | | | |
| *Paracyathus adetos* | | | x | x | x | x | x | | | | | | | | | x | x | x | x |
| *Oxysmilia pliocenica* | | | | | | | | | | | | | | | | | | x | |
| *Asterosmilia profunda* | x | | | | | | | x | x | x | x | | x | | | | | | |
| *Asterosmilia irregularis* | | | | | | | | | | | | | | | | | | | |
| *Asterosmilia exarata* | | | | | | | | | | | x | x | | | | | | | |
| *Sphenotrochus hancocki* | | | | | | | | | | | | | | x | | | | | |
| *Gardineria minor* | | | | | | | | | | | | | | | | | | | |
| *Guynia annulata* | | | | | | | | | | | | | x | | | | | | |
| *Schizocyathus fissilis* | | | | | | | | | | | | | | | | | | | |
| *Balanophyllia pittieri* | | | | | | x | | | | | | | | | x | | | | |
| *Stylaster roseus* | | x | | | | | | | | | | | | | | | | | |

tors have somewhat broad bathymetric ranges, a restricted (or narrower) range was calculated based upon the overlap of the ranges of the species being considered. For example, if a similar extant counterpart species is known to occur at 10–50 m and another species from 20–60 m, the hypothetical restricted range (overlap) of the formation in which they both occur would be 20–50 m. The same method was used by Cairns (1979) to infer restricted bathymetric ranges of Recent deep-water corals that were based on collecting stations some of which covered a broad range of depths.

## RESULTS

### BIODIVERSITY

The most diverse fossil azooxanthellate coral fauna known from the Caribbean consists of 20 species from the Dominican Republic (Cairns and Wells, 1987). Slightly less diverse faunas are known from the Caribbean Panamanian Neogene (15 stony coral species) and from the Caribbean Costa Rican Neogene (11 species). Taken together, a total of 18 fossil azooxanthellate stony coral species are known from this southern Central American region (Table 1). All 15 species from Panama are new records for that country (Table 1), whereas four of the 11 species from Costa Rica were previously reported from Limon, primarily by Vaughan (1919): *Asterosmilia exarata* Duncan, 1867 (as *A. hilli* Vaughan, 1919); *Balanophyllia pittieri* Vaughan, 1919; *Sphenotrochus* sp. cf. *S. hancocki* Durham and Barnard, 1952 (as *S. intermedius* by Wells, 1983); and *Archohelia limonensis* Vaughan, 1919. In addition to the Dominican Republic and Pan-

Table 2.—Continued.

| | 357 | 358 | 359 | 368 | 379 | 422 | 423 | 451 | 458 | 465 | 466 | 468 | 475 | 478 | 479 | 481 | 627 | 634 | 635 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Septastraea altispina* | | | | | x | x | | | | | | | | | | | | | |
| *Septastraea marylandica* | | | | | | | | | | | | | | | | | | | |
| *Antillocyathus gracilis* | x | | | | | | x | | | | | | x | | | | | | |
| *Antillocyathus cristatus* | | | | | | | | x | x | | | | | | | | | | |
| *Trochocyathus chevalieri* | | x | | | | | | | | | | | | | | | x | | |
| *Paracyathus henekeni* | | | | | | | | | | | | | | | | | | | |
| *Paracyathus adetos* | | | | | | | | | | | | | x | | | | | | |
| *Oxysmilia pliocenica* | | | | | | | | | | | | | | | | | | | |
| *Asterosmilia profunda* | | | x | x | | | | | | | | | | x | x | x | | | |
| *Asterosmilia irregularis* | | | | | | | | | | | | | | | | | x | | |
| *Asterosmilia exarata* | | x | | x | | | | | | | | x | | | | | x | | |
| *Sphenotrochus hancocki* | | | | x | | | | | | | | | | | | | | | |
| *Gardineria minor* | | | | | | | | | | | x | | | | | | | | |
| *Guynia annulata* | | | | | | | | | | | | | | | | | | | x |
| *Schizocyathus fissilis* | | x | | | | | | | | | | | | | | | | | |
| *Balanophyllia pittieri* | | | | | | | | | | x | x | x | | | | | x | | x |
| *Stylaster roseus* | | | | | | | | | | | | | | | | | | x | |

Table 2.—Continued.

| 198 | 201 | 205 | 208 | 212 | 294 | 295 | 298 | 306 | 307 | 308 | 310 | 311 | 313 | 324 | 326 | 334 | 335 | 339 | 345 | 346 | 348 | 350 | 352 | 355 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  |  |  |  |  |  |  |  |  |  | x | x |  |  |  |  |  |  |  |  |  |
|  | x |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| x |  |  | x |  | x | x | x | x | x | x |  | x |  |  |  |  | x |  |  | x | x | x |  | x |
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|  |  |  |  |  | x | x | x |  |  | x |  |  | x |  |  | x |  |  | x |  |  | x |  |  |
| x |  | x |  |  |  |  |  | x | x |  |  | x |  |  |  |  |  |  |  |  |  |  | x |  |
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| x |  |  |  |  |  |  |  |  |  |  | x |  |  |  |  |  | x |  |  |  |  |  |  |  |
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amanian-Costa Rican areas, other localities within the Caribbean region (Table 1) from which Neogene azooxanthellate Scleractinia have been reported include: Colombia (Vaughan, 1919), Venezuela (Weisbord, 1968), Trinidad (Vaughan and Hoffmeister, 1926), Carriacou (Wells, 1971), Martinique (Wells, 1945), and Jamaica (Duncan, 1864; Vaughan, 1919; Cairns and Wells, 1987).

Budd *et al.* (1994) reported 175 species of zooxanthellate corals from the Caribbean Neogene through Recent, and 142 species of azooxanthellates are known from the same time period and region, resulting in a total of 317 species. The 101 azooxanthellate species known from the Recent are listed in Table 4 and the 49 fossil azooxanthellate scleractinian species are listed in Table 1, eight species common to both lists. There are, as yet, no Caribbean stylasterid species known exclusively from the fossil record (Table 5). Of the 175 zooxanthellate species reported by Budd *et al.* (1994), 23 or 13% are as yet undescribed, and 18 (also 13%) of the 142 azooxanthellates are undescribed.

## TURNOVER RATES

Text-figures 1–2 illustrate the stratigraphic ranges of the 50 azooxanthellate stony coral species known from the Caribbean Neogene and Table 6 summarizes the numbers of origins and extinctions together with species and generic richness for the Neogene to Recent. When taxa found at only one locality or time level are omitted in order to decrease signal "noise" (species 1, 3, 6, 11, 13–15, 18, 20, 22, 23, 27–33, 35, 38–40, 43, 49), and the apparent sudden diversity increase of Re-

Table 2.—Continued.

| 639 | 640 | 642 | 646 | 670 | 708 | 710 | 720 | 738 | 757 | 766 | 767 | 962 | 1101 | 1102 | 1103 | 1104 | 1105 | 1107 | 1118 | 1119 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
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|  |  | x | x |  |  |  |  |  | x |  | x | x |  |  |  |  |  |  |  |  |
|  |  | x |  |  |  |  |  |  | x |  |  |  | x | x | x | x | x | x | x | x |
| x | x | x | x |  |  |  |  |  | x |  | x | x |  |  |  |  |  |  |  |  |
|  |  |  |  | x |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
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|  | x | x | x |  |  |  |  |  | x | x | x | x |  |  |  |  |  |  |  |  |
| x |  |  |  |  | x | x | x | x |  |  |  |  |  |  |  |  |  |  |  |  |

Table 3.—Inferred bathymetric ranges, general gross morphological characters, and stratigraphic occurrences of 10 Neogene Panamanian-Costan Rican azooxanthellate stony corals.

| Neogene species | Recent counterpart | Depth range (m) of counterpart | Attached/ unattached | Colonial/ solitary | Formations |
|---|---|---|---|---|---|
| *Septastraea altispina* | *Astrangia conferta* | 9–37 | A | C | CA, SHP |
| *Septastraea marylandica* | *Astrangia conferta* | 9–37 | A | C | CA |
| *Stylaster roseus* | * | 1–73 | A | C | CA, Mn |
| *Balanophyllia pittieri* | *Balanophyllia grandis* | 40–96 | U | S | CA, Mn |
| *Asterosmilia exarata* | *Asterosmilia marchadi* | 32–229 | U | S | CA, EV, Mn |
| *Gardineria minor* | * | 2–242 | A | S | Mn |
| *Spheno.* cf. *hancocki* | *Sphenotrochus hancocki* | 18–274 | U | S | EV, Mn, RB |
| *Oxysmilia pliocenica* | *Oxysmilia rotundifolia* | 46–640 | A | S | CA |
| *Guynia annulata* | * | 28–653 | U | S | CA, EV, Mn |
| *Schizocyathus fissilis* | * | 88–1300 | U | S | EV |

* Counterpart species same as Neogene species.
CA, Cayo Agua Formation; SHP, Shark Hole Point Formation; Mn, Moin Formation; EV, Escudo de Veraguas Formation; RB, Rio Banano Formation.
A, attached; U, unattached.
C, colonial; S, solitary.

cent species is ignored, it appears that the highest species origination rate occurs in the Middle to Late Miocene, and the highest extinction rate in the Late Pliocene, resulting in the highest species and generic richness in the early Late Pliocene. The sudden increase in Recent species and genera is discussed below.

The high species turnover rate in the Late Miocene to early Late Pliocene is especially apparent in the Caryophylliidae, whereas most species in the Rhizangiidae, Guyniidae, and Dendrophylliidae appear to be longer-lived (Text-fig. 1). In the case of the Dendrophylliidae, however, these results may be influenced by the difficulty of discriminating fossil species. No azooxanthellate species is known to have crossed the Oligocene–Miocene boundary. Twenty-four azooxanthellate scleractinian genera occurred in the Caribbean Neogene (Table 1), only three of which do not also occur in the Recent: *Septastraea, Antillocyathus,* and *Dominicotrochus.*

## Paleoecology

Four of the 18 Panamanian–Costa Rican Neogene stony corals are also known from the Recent and an additional six species have closely related, if not identical, counterparts in the Recent. These 10 species are listed in Table 3 in order of their shallowest to deepest maximum depth ranges of the Recent or counterpart species. Table 3 also lists whether the species is unattached or attached, colonial or solitary, and the formations in which it was found. The restricted depth range (see Material and Methods) for the Cayo Agua Formation (Appendix A, Map 6 and Insets; Appendix B, Sections 16–20) is 37–46 m; Moin Formation, Lomas del Mar (Appendix A, Inset B of Map 11; Appendix B, Section 36), 40–73 m; and Escudo de Veraguas Formation (Appendix A, Map 4, Insets A–C; Appendix B, Sections 10–11), 88–229 m. It is acknowledged that the actual range of a fossil assemblage is probably broader than this rather conservatively determined figure, and that the depth ranges of extant species is incomplete and not necessarily directly applicable to the Pliocene epoch. Other assumptions implicit in this method are that the fossil species actually co-occurred in the formation and that the water depth within the formation did not appreciably change over time. Nonetheless, in an analysis based on foraminiferal assemblages, Collins (1993) and Collins *et al.* (1995) found similar inferred bathymetric ranges for the Cayo Agua Formation (20–80 m), Moin Formation, Lomas del Mar (50–100 m), and the Escudo de Veraguas Formation (100–150 m).

Using the same method described above, the restricted depth range of fossil species having attached coralla is 37–82 m and unattached coralla, 88–96 m, suggesting that greater depth (*e.g.,* a higher probability of a soft substrate) favors unattached coralla. The restricted range for colonial species is 37–40 m and for solitary species, 82–88 m, suggesting that greater depth favors solitary coralla. Among the 114 extant azooxanthellate scleractinian genera, two-thirds have solitary coralla and one-third have colonial coralla. All of the colonial genera consist of species that are attached, whereas only 37% of the solitary genera consist of attached species, 51% of unattached species, 3% of a mixture, and 9% of transversely dividing species. To date there has been no study correlating generic depth ranges to growth form: both solitary and colonial as well as attached and unattached species and

Table 4.—List of the 101 species of Recent Caribbean azooxanthellate Scleractinia, taken primarily from Cairns (1979) and Hubbard and Wells (1986). An asterisk (*) indicates that the species is known to occur in water depths of less than 183 m, and a cross (+) signifies that the species has a fossil record and thus is also listed in Table 1.

*_Agaricia cailleti_
*_Anomocora fecunda_
_Anthemiphyllia patera_
*_A. rathbuni_
*_Astrangia solitaria_
*_Asterosmilia marchadi_
*_A. prolifera_
*_Balanophyllia bayeri_
*_B. caribbeana_
*_B. cyathoides_
*_B. dineta_
*_B. floridana_
*_B. goesi_
*_B. grandis_
_B. hadros_
*_B. palifera_
_B. wellsi_
_Caryophyllia ambrosia caribbeana_
*_C. antillarum_
_C. barbadensis_
*_C. berteriana_
*_C. cornuformis_
_C. corrugata_
*_C. parvula_
_C. paucipalata_
_C. polygona_
*_C. zopyros_
*_Cladocora debilis_
*_Coenosmilia arbuscula_
*_Colangia immersa_
_Concentrotheca laevigata_
_Crispatotrochus cornu_
*_Dasmosmilia variegata_
_Deltocyathus agassizi_
*_D. calcar_
_D. eccentricus_
+_D. italicus_
_D. moseleyi_
_D. pourtalesi_
_Dendrophyllia alternata_
+*_D. cornucopia_
*_D. gaditana_
_D. alternata_
*_Desmophyllum cristagalli_
*_D. striatum_
_Enallopsammia profunda_
_E. rostrata_
_Flabellum atlanticum_
_F. moseleyi_
_Fungiacyathus crispus_
_F. marenzelleri_
_F. pusillus_
_F. symmetricus_
+*_Gardineria minor_
*_G. paradoxa_
*_G. simplex_
+*_Guynia annulata_
*_Javania cailleti_
_J. pseudoalabastra_
_Labyrinthocyathus langae_
_Leptopenus discus_
*_Leptopsammia trinitatis_
*_Lophelia prolifera_
*_Madracis myriaster_
*_M. asperula_
*_M. brueggemanni_
*_M. pharensis pharensis_
*_Madrepora carolina_
*_M. oculata_
*_Oxysmilia rotundifolia_
+*_Paracyathus pulchellus_
*_Phacelocyathus flos_
+*_Phyllangia americana_
_Peponocyathus folliculus_
*_P. stimpsonii_
_Placotrochides frustum_
*_Polycyathus mullerae_
*_P. senegalensis_
*_Polymyces fragilis_
+_Pourtalocyathus hispidus_
*_Pourtalosmilia conferta_
*_Rhizopsammia manuelensis_
*_Rhizosmilia gerdae_
*_R. maculata_
+*_Schizocyathus fissilis_
_Solenosmilia variabilis_
*_Sphenotrochus auritus_
*_Stenocyathus vermiformis_
_Stephanocyathus coronatus_
_S. diadema_
_S. laevifundus_
_S. paliferus_
*_Tethocyathus cylindraceus_
_T. recurvatus_
_T. variabilis_
*_Thalamophyllia riisei_
_Trematotrochus corbicula_
*_Trochocyathus rawsonii_
_T. fossulus_
_T. fasciatus_
_Trochopsammia infundibulum_
*_Tubastraea coccinea_

Table 5.—Numbers of species of Neogene to Recent Caribbean Scleractinia and Stylasteridae reported as zooxanthellate and azooxanthellate components.

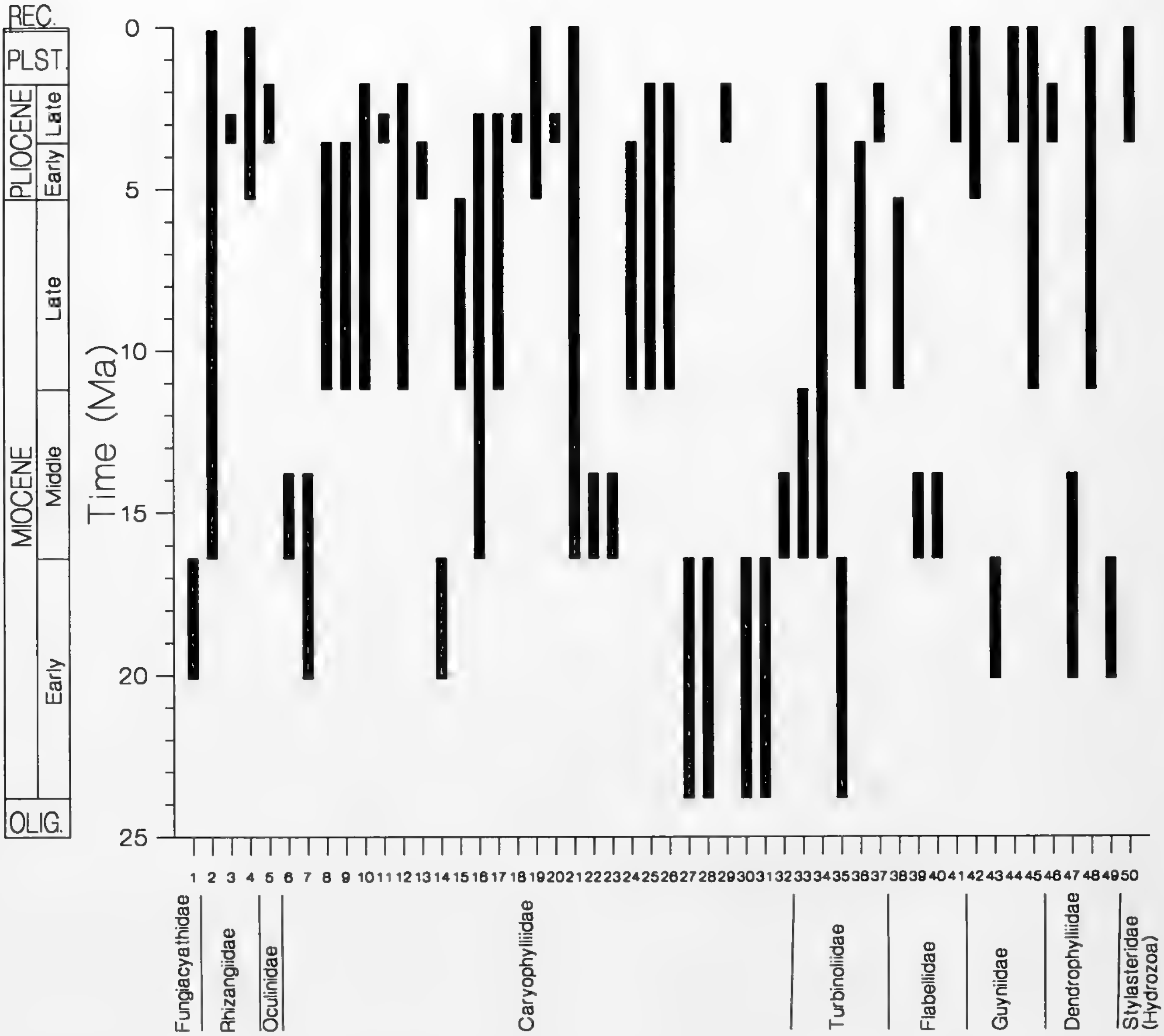
| | Zooxan-thellate | Azooxan-thellate | Total Sclerac-tinia | Stylas-teridae |
|---|---|---|---|---|
| Neogene to Recent | 175 | 142 | 317 | 42 |
| Recent | 68 | 101 | 169 | 42 |
| Exclusively Recent | 18 | 93 | 111 | 41 |

genera occur at a broad range of depths (*i.e.*, 0–2000 m). Nonetheless, the data presented in Table 3 suggest that attached colonial coralla are more common in shallow water, whereas solitary and unattached species occur in deeper water. Consideration of inferred depth, coloniality, and attachment shows a consistent trend within the three studied Caribbean formations. The assemblage from the Cayo Agua Formation is inferred to be the shallowest (37–46 m), its stony coral fauna consisting of two colonial attached, three solitary attached, and six solitary unattached species. The Moin Formation (Lomas del Mar section) is inferred to be of intermediate depth (40–73 m), its assemblage consisting of one colonial attached and seven solitary unattached species. The Escudo de Veraguas Formation is inferred to be the deepest assemblage among the three (88–229 m), containing exclusively solitary unattached species. Nonetheless, in the broader context of all azooxanthellate corals, these three formations are typical of a relatively shallow-water fauna; in the Recent fauna, azooxanthellates are more common at slope depths (especially 200–800 m), one species (*Leptopenus discus* Moseley, 1881), occurring as deep as 3475 m in the Caribbean (Cairns, 1979).

## DISCUSSION

The uneven numbers of fossil azooxanthellate species from various regions of the Caribbean (Table 1) reflect the uneven collecting efforts made in those regions, the Dominican Republic and Panama being the most intensively sampled and thus having the highest species richness. The taxonomic composition of the list of 50 fossil species also shows a decided preponderance of shallow-water (<183 m) species, except for those species reported from the Early to Middle Miocene of Carriacou (Wells, 1971), which include primarily deeper water (bathyal) genera and species.

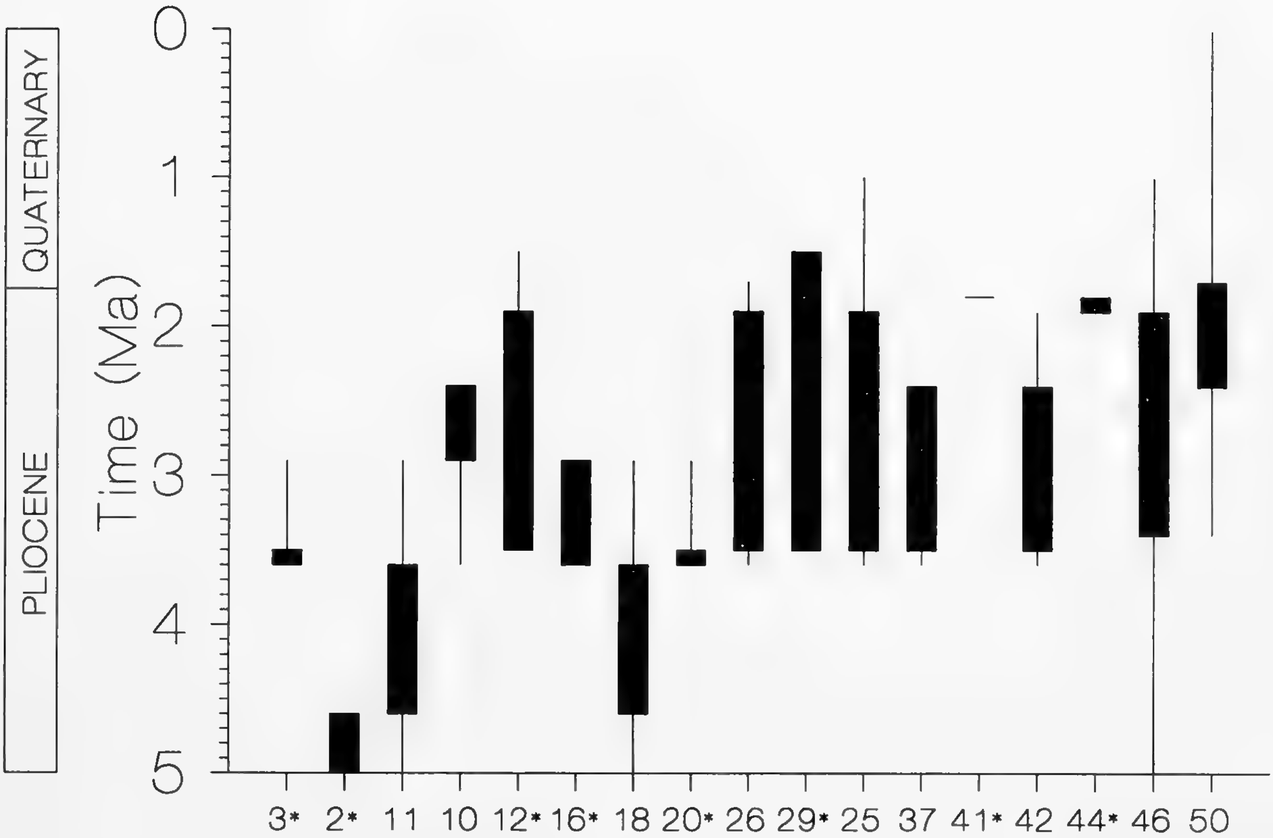
Azooxanthellate species constitute 45% (142/317) of the Caribbean Neogene to Recent scleractinian fauna (Table 5), which is probably a low estimate, since the deeper water fossil species are poorly known. By comparison, in the Recent fauna, for which the deep-



Text-figure 1.—Stratigraphic ranges for all Caribbean azooxanthellate stony corals that have a fossil record in the Neogene. Taxa arranged by families. Numbers for species correspond with those in Table 1.

and shallow-water species are well known, Cairns (1979: Table 5) found that azooxanthellates constituted 66% (116/177 species) of the tropical western Atlantic scleractinian fauna. If a similar ratio were applied to the Caribbean Neogene–Recent coral fauna, one might expect to find 340 (instead of 142) azooxanthellate species in addition to the 175 reef species.

The almost order of magnitude increase in species originations and species and generic richness for Recent azooxanthellates (Table 6) is not interpreted as an evolutionary explosion, but rather as the common paleontological collecting artifact known as the "pull of the Recent". Most of the fossil azooxanthellates known from the Caribbean were inferred to have lived at shelf depths (≤183 m) (see Paleoecology section), a facies more likely to be preserved on land than a deeper water facies. However, 42% of the Recent Caribbean azooxanthellates (Table 4) occur deeper than 183 m exclusively, many species are restricted to the lower slope, and one species, *Leptopenus discus*, occurs as deep as 3475 m. This large segment of the azooxanthellate fauna is relatively well known in the Recent (Cairns, 1979) but virtually unknown in the fossil record. Consistent with this explanation, Chevalier (1961) reported 112 azooxanthellate species from the Mediterranean Miocene, a fauna character-



Text-figure 2.—Age ranges of coral species in PPP samples. Species numbered as in Table 1. Line = maximum range. Bar = minimum range, except for starred species, where bar = interval within which the species occurs.

ized by many deep-water genera. Also in this context, only one of the 42 Recent species of western Atlantic stylasterids occurs in shallow water (Cairns, 1983), *i.e., Stylaster roseus,* which is also the only species known from the fossil record. Another reason for the small number of fossil azooxanthellates may be due to the small size of their corallum, some solitary species having an adult calicular diameter of only 1 mm.

Table 6.—Estimates of species richness and numbers of origins and extinctions of Caribbean azooxanthellate Scleractinia. Richness estimated by using range-through method. Numbers in parentheses represent number of species known from only one locality.

| | Origins | Extinctions | Total number of species | Total number of genera |
|---|---|---|---|---|
| Recent | 93 | | 101 | 51 |
| Pleistocene | 0 | 1 (0) | 9 | 9 |
| Late Pliocene | 3 (1) | 9 (1) | 18 | 15 |
| early Late Pliocene | 7 (4) | 6 (4) | 21 | 14 |
| Early Pliocene | 4 (1) | 5 (1) | 19 | 11 |
| Late Miocene | 13 (2) | 2 (2) | 17 | 11 |
| Middle Miocene | 11 (7) | 9 (7) | 13 | 10 |
| Early Miocene | 11 (9) | 9 (9) | 11 | 8 |

## CONCLUSIONS

A total of 142 azooxanthellate scleractinian species are known from the Caribbean Neogene and Recent based upon new collections from the Pliocene of Panama and Costa Rica and previous literature. Forty-one of those 142 species are known exclusively from fossils, and of the remaining 101 extant species, only eight have a fossil record. One stylasterid is also known from the Caribbean Neogene. Adding the 175 species of reef (zooxanthellate) species reported by Budd *et al.* (1994) results in 317 known species of Scleractinia from the Caribbean Neogene to Recent. The number of fossil azooxanthellates is considered to be relatively low because lithologies consisting of shallow-water (continental shelf) facies have been predominantly studied thus far; most Recent azooxanthellates occur in deeper (continental slope) water. The highest known species diversities of fossil azooxanthellate stony corals within the Caribbean region are in the Dominican Republic (20 species) and Panama (15 species). Examination of the stratigraphic ranges of the azooxanthellate coral species suggests that the highest origination rate occurred in the Middle to Late

Miocene, and that the highest extinction rate occurred in the Late Pliocene, following a maximum of both generic and specific taxonomic diversity in the early Late Pliocene. Using depth ranges of fossil taxa inferred from those of the same or closely related extant species, it is suggested that the Panamanian Cayo Agua Formation supported corals living at depths of 37–46 m, the Costa Rican Moin Formation at depths of 40–73 m, and Panamanian Escudo de Veraguas Formation at depths of 88–229 m, the three formations listed in order from shallowest to deepest.

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# CHAPTER 7

# PLIOCENE TO PLEISTOCENE REEF CORAL ASSEMBLAGES IN THE LIMON GROUP OF COSTA RICA

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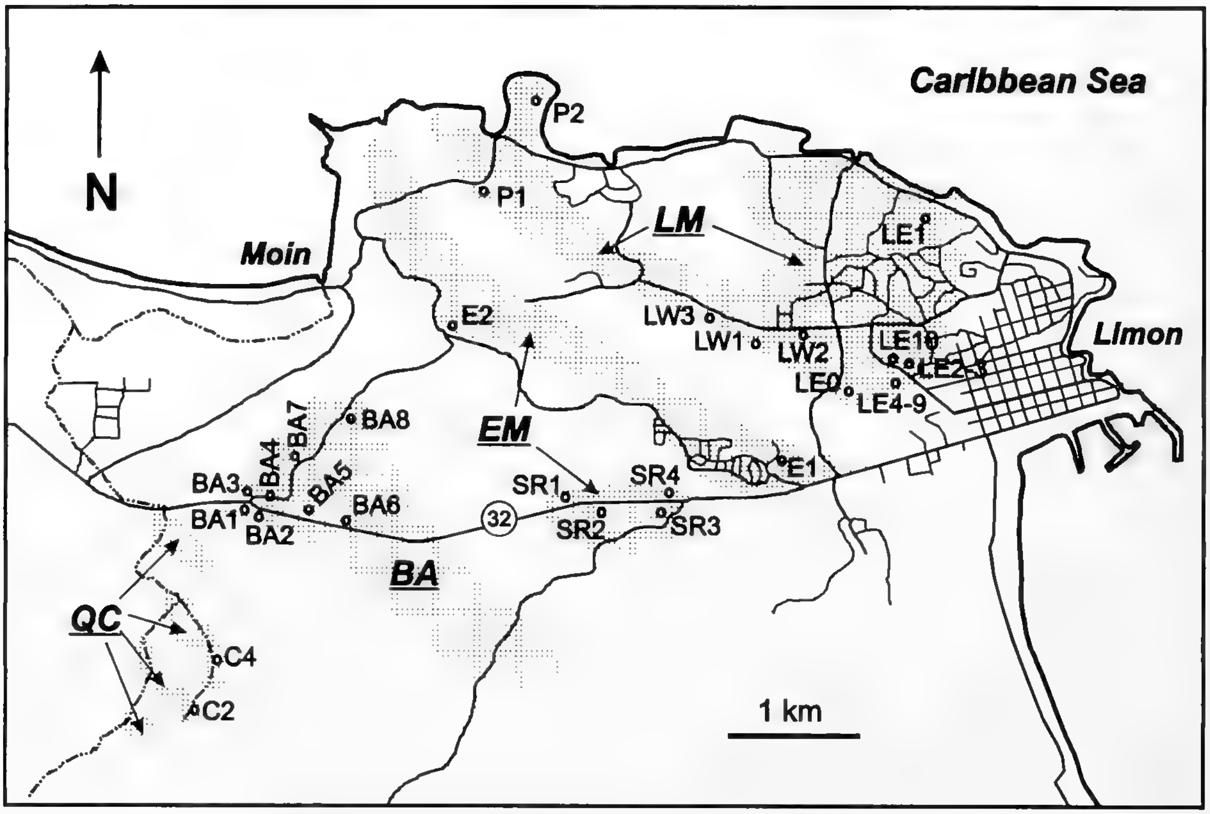
## INTRODUCTION

The Pliocene through Pleistocene sequence in the Limon Group of Costa Rica provides some of the richest and best preserved fossil material documenting an episode of accelerated evolution that transformed the Caribbean reef coral fauna between 4 and 1 Ma (Budd *et al.,* 1994a; Johnson *et al.,* 1995; Budd *et al.,* 1996; Jackson *et al.,* 1996; Budd and Johnson, 1997). During faunal turnover, approximately 80% of the >100 Mio-Pliocene reef coral species (32% of 38 genera) living in the Caribbean became extinct, and >60% of the species now living in the region originated. The pattern of turnover was unusual in that increased speciation preceded increased extinction by 1–2 million years. As a consequence, reef assemblages consisted locally and regionally of a mix of extinct and living species. To better understand the cause of turnover and the complex pattern of evolutionary events involved, we have been making large, bed-by-bed collections of reef corals through well-preserved Plio-Pleistocene reef sequences at scattered Caribbean locations and comparing patterns of replacement across the region. The purpose of this paper is to describe collections of reef corals made through reefal portions of the Limon sequence of Costa Rica during four initial field expeditions, and to discuss their potential for future analysis of faunal turnover.

In the Limon sequence, reef corals occur in three formations (the Rio Banano, Quebrada Chocolate, and Moin formations) that crop out in small, isolated exposures near the town of Limon. Each of these three formations contains one or more reef 'trends', which consist of a continuous series of coral buildups aligned parallel to paleoshoreline (Text-fig. 1). As detailed in McNeill *et al.* (in press) and Coates (this volume), the reef trends become progressively younger from southwest to northeast, and appear to correspond in timing with eustatic sea level highstands. The oldest known buildup in the sequence, the Brazo Seco 'patch', occurs within the Rio Banano Formation, and preliminary strontium-isotope analyses suggest that it has an Early



Text-figure 1.—Map of the Limon area showing four of the five reef trends (shaded) and the locations of 33 of the 34 analyzed localities. Locality BS (Brazo Seco trend) is located along Quebrada Brazo Seco approximately 13 km due west of C4. Locality abbreviations are given in Table 1. QC, Quebrada Chocolate trends; BA, Buenos Aires trend; EM, Empalme trend (including Santa Rosa patch); LM, Lomas del Mar trend.

Pliocene age between 5.2–4.3 Ma (McNeill *et al.,* in press). Two more extensive trends, the Quebrada Chocolate and Buenos Aires trends, occur within the Quebrada Chocolate Formation. A combination of age-diagnostic biostratigraphic markers (planktic foraminifera, nannofossils), strontium-isotope age ranges, and magnetic polarity data indicate an early Late Pliocene age between 3.5–3.3 Ma for the Quebrada Chocolate trend, and 3.2–2.9 Ma for the Buenos Aires trend (McNeill *et al.,* 1997; McNeill *et al.,* in press; Coates, this volume). The two youngest trends, the Empalme and Lomas del Mar trends, occur within the Moin Formation. A combination of age-diagnostic biostratigraphic markers (planktic foraminifera, nannofossils), strontium-isotope age ranges, and magnetic polarity data indicate a Plio-Pleistocene age between 2.9–1.9 Ma for the Empalme trend (including the Santa Rosa patch), and 1.9–1.5 Ma for the Lomas del Mar trend (McNeill *et al.,* in press; Coates, this volume). Despite apparent gaps in the sequence at 4.3–3.3 Ma as well as between the respective reef trends, the trends completely bracket the period of Caribbean faunal change, and thus provide valuable information for understanding patterns of species evolution within the basin during faunal turnover.

Collections of ‘hermatypic’ or ‘reef-building’ corals (zooxanthellate members of the Order Scleractinia, Class Anthozoa, Phylum Cnidaria) were made through the Limon reefal units as part of four field expeditions associated with the Panama Paleontology Project (PPP): (1) April 1989 (233 specimens, 49 species), (2) January 1992 (302 specimens, 37 species), (3) March 1992 (647 specimens, 55 species), and (4) July 1993 (1209 specimens, 76 species). During these different expeditions and on different days within the same expedition, samples were taken both from newly discovered sites and from previously sampled sites. The collected specimens were shipped to the University of Iowa, prepared, identified to species, and entered into a specimen database that is available on the World-Wide Web at http://nmita.geology.uiowa.edu. Although currently still at the University of Iowa, most of the material will be deposited at the U. S. National Museum of Natural History, Department of Invertebrate Zoology (NMNH). Selected voucher specimens of each species will be deposited at the Paleontology Repository of the Department of Geology, University of Iowa (SUI), and at the Escuela de Biología of the University of Costa Rica. Altogether, the collections comprise 2392 specimens (2356 identifiable to species) and 82 species. Prior to 1989, the only published faunal list of fossil reef corals from the Limon region was that of Vaughan (1919), who recorded only four species and one variety. Since 1993, additional collections of reef corals have been made in the region on two subsequent PPP-associated expeditions (February 1995, July 1996); these newer collections are still in the process of being prepared and identified, and are therefore not included herein.

As part of our description of the Limon collections, we provide details on sampling methods and consider potential biases that these methods pose for quantitatively analyzing species evolution and community change through geologic time. In contrast to other fossil groups treated in this volume, reef coral specimens are typically large in size (sometimes over a 0.5 m in diameter) and therefore cannot be sampled using conventional bulk sampling procedures. Furthermore, because specimens are often worn and fragmented, species are difficult to identify in the field, especially in pre-Quaternary deposits such as those treated herein. In addition, reefal units tend to be relatively rapidly deposited and patchily distributed through space and time; therefore, long, continuous sequences are rare. Because of their symbiotic algae, diverse accumulations of reef corals are generally restricted to depths of <40–50 m, where microfossils that are most useful in biostratigraphy are poorly preserved (see Budd and Kievman, in press). As a consequence, estimated age dates are low in resolution.

Given these difficulties, we provide preliminary analyses of data derived from the collections to assess the diversity and abundance of reef coral taxa within the Limon reef sequence and to provide a general overview of the fauna. In this assessment, we use numbers of species (*i.e.*, species richness) to estimate coral diversity, and numbers of specimens per species to estimate relative abundance. Other than species richness, we do not attempt to calculate diversity indices because of sampling inconsistencies. We examine frequencies of different colony shapes to provide a rough interpretation of the paleoenvironments of different reef trends, and we compare global first and last occurrences of species among trends to evaluate the evolutionary significance of the fauna. We analyze the assemblages using multivariate statistical procedures (cluster analysis, detrended correspondence analysis) to describe patterns of replacement and faunal change within the Limon region during Plio-Pleistocene turnover. Lastly, to present a broader picture of Neogene and earliest Quaternary reef faunas along the northeastern Costa Rican and Panamanian coast, we provide descriptions of small initial PPP collections from the Bocas del Toro region of Panama. Our conclusions focus on the significance of the Limon reef fauna in understanding Plio-Pleistocene faunal turnover across the entire Caribbean region.

We emphasize that the analyses presented herein are preliminary and exploratory in nature, and were performed mainly to assess the potential for more rigorous faunal analysis in the future. In future analyses, Borne and Budd plan to compare coral and ostracode assemblages to interpret reef environments more precisely. Quadrat or line transect sampling methods (see Budd *et al.*, 1989; Stemann and Johnson, 1992; Pandolfi, 1996) also need to be applied at selected well-preserved exposures to evaluate more accurately diversity, relative abundance, and species associations.

## ACKNOWLEDGMENTS

We are especially grateful to Jeremy Jackson and Tony Coates for bringing our attention to these exceptional exposures of Plio-Pleistocene reef corals; and to Tony Coates, Don McNeill, Pam Borne, and Jorge Obando for providing the stratigraphic and sedimentologic framework for our work. We thank Harry Filkhorn, Terry Hughes, John Pandolfi, and Brian Rosen for reviewing the manuscript; Alan Cheetham for statistical advice; J. Cortés, P. Denyer, J. Wineberg-Swedberg, S. Schellenberg for help with field work; J. Golden, K. Ketcher, K. Saville, T. Coffer, and S. Cairns for help with specimen preparation and curation; and Y. Ventocillo, H. Fortunato, and X. Guerra for help with shipping and integrating our collections into the PPP Database, maps and stratigraphic sections.

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## DEFINITIONS OF TERMS

Because our collecting methods differ from those employed for other fossil groups, our usage of collection-related terms is unique and requires explanation. In our work, an *'individual specimen'* is defined as a single colony (or fragments of what was presumed to

Table 1.—List of 1989–1993 Costa Rica and Panama zooxanthellate coral collection sites arranged in stratigraphic order from oldest to youngest.

| Field number | PPP number | Site name | Strat. section number | Number of specimens | Number of species | Formation | Reef trend | Locality code |
|---|---|---|---|---|---|---|---|---|
| **Costa Rica:** | | | | | | | | |
| AB93-05 | 1381 | Brazo Seco | none | 57 | 19 | Rio Banano | Brazo Seco | BS |
| AB93-67 | 1386 | Q. Chocolate | 33 | 10 | 6 | Q. Chocolate | Q. Chocolate | C2 |
| AB93-68 | 1384 | Q. Chocolate–road | 33 | 65 | 27 | Q. Chocolate | Q. Chocolate | C4 |
| AB93-37 | 1347 | Rt. 32–Dole | 33 | 3 | 3 | Q. Chocolate | Buenos Aires | BA1 |
| AB93-49 | 1359 | Rt. 32–CTA fence | 33 | 6 | 5 | Q. Chocolate | Buenos Aires | BA1 |
| AB93-50 | 1360 | Rt. 32–CTA fence | 33 | 1 | 1 | Q. Chocolate | Buenos Aires | BA1 |
| AB93-70-1 | 1387 | Rt. 32–CTA fence | 33 | 10 | 4 | Q. Chocolate | Buenos Aires | BA1 |
| AB93-06 | 1316 | Rt. 32–CTA fence | 33 | 41 | 15 | Q. Chocolate | Buenos Aires | BA2 |
| AB93-52 | 1362 | Rt. 32–CTA fence | 33 | 8 | 7 | Q. Chocolate | Buenos Aires | BA2 |
| AB93-70-2 | 1388 | Rt. 32–CTA fence | 33 | 37 | 12 | Q. Chocolate | Buenos Aires | BA2 |
| AB93-36 | 1346 | Old Moin Road–south | 33 | 9 | 7 | Q. Chocolate | Buenos Aires | BA3 |
| AB93-53 | 1363 | Old Moin Road–south | 33 | 2 | 1 | Q. Chocolate | Buenos Aires | BA3 |
| KJ-C-1 | 1125 | Old Moin Road–south | 33 | 19 | 12 | Q. Chocolate | Buenos Aires | BA3 |
| AB93-35 | 1345 | Old Moin Road–south | 33 | 9 | 9 | Q. Chocolate | Buenos Aires | BA4 |
| AB93-54 | 1364 | Old Moin Road–south | 33 | 6 | 3 | Q. Chocolate | Buenos Aires | BA4 |
| AB93-55 | 1365 | Old Moin Road–south | 33 | 2 | 2 | Q. Chocolate | Buenos Aires | BA4 |
| AB93-60 | 1370 | Rt. 32–Chiquita | 33 | 2 | 1 | Q. Chocolate | Buenos Aires | BA5 |
| AB93-38 | 1348 | Rt. 32–La Colina | 33 | 20 | 9 | Q. Chocolate | Buenos Aires | BA6 |
| KJ-32-1 | 1124 | Rt. 32 | 33 | 94 | 15 | Q. Chocolate | Buenos Aires | BA6 |
| AB93-32 | 1342 | Moin flat field–sw | 33 | 35 | 17 | Q. Chocolate | Buenos Aires | BA7 |
| AB93-33 | 1343 | Moin flat field–mid | 33 | 21 | 13 | Q. Chocolate | Buenos Aires | BA7 |
| AB93-34 | 1344 | Moin flat field–mid | 33 | 69 | 28 | Q. Chocolate | Buenos Aires | BA7 |
| AB93-56 | 1366 | Moin flat field–north | 33 | 35 | 15 | Q. Chocolate | Buenos Aires | BA7 |
| AB93-31 | 1341 | Old Moin Road–north | 33 | 21 | 13 | Q. Chocolate | Buenos Aires | BA8 |
| TS-CR-8 | 719 | Pueblo Nuevo | 34 | 30 | 24 | Moin | Santa Rosa | SR1 |
| AB93-63 | 1373 | Rt. 32–swimming pool | 34 | 33 | 14 | Moin | Santa Rosa | SR2 |
| JW93-16 | 1499 | Rt. 32–swimming pool | 34 | 16 | 10 | Moin | Santa Rosa | SR2 |
| JW93-17 | 1500 | Rt. 32–swimming pool | 34 | 12 | 7 | Moin | Santa Rosa | SR2 |
| TS-CR-7 | 715 | Pueblo Nuevo | 34 | 13 | 11 | Moin | Santa Rosa | SR2 |
| AB93-41 | 1351 | Rt. 32–stadium | 34 | 36 | 18 | Moin | Santa Rosa | SR3 |
| AB93-62 | 1372 | Santa Rosa Road | 34 | 20 | 14 | Moin | Santa Rosa | SR3 |
| AB93-57 | 1367 | Rt. 32–Santa Marta Soda | 34 | 23 | 13 | Moin | Santa Rosa | SR4 |
| AB93-84 | 1428 | Pueblo Nuevo | 34 | 9 | 6 | Moin | Empalme | E1 |
| AB93-30 | 1340 | Old Moin Road–north | 34 | 4 | 4 | Moin | Empalme | E2 |
| AB93-64 | 1374 | Corales 1–Tajo | 36 | 18 | 10 | Moin | Lomas del Mar | LE0 |
| AB93-39 | 1349 | St. Eduviges | 36 | 12 | 8 | Moin | Lomas del Mar | LE1 |
| AB93-40 | 1350 | ocean view | 36 | 2 | 1 | Moin | Lomas del Mar | LE1 |
| TS-CR-5 | 771 | St. Eduviges | 36 | 15 | 12 | Moin | Lomas del Mar | LE1 |
| TS-CR-6 | 772 | St. Eduviges | 36 | 12 | 10 | Moin | Lomas del Mar | LE1 |
| TS-CR-9 | 646 | Lomas del Mar | 36 | 135 | 31 | Moin | Lomas del Mar | LE2 |
| TS-CR-1 | 639 | Lomas del Mar | 36 | 28 | 12 | Moin | Lomas del Mar | LE3 |
| CJ-92-06-21 | 962 | Lomas del Mar | 36 | 146 | 29 | Moin | Lomas del Mar | LE4 |
| CJ-92-06-22 | 963 | Lomas del Mar | 36 | 96 | 19 | Moin | Lomas del Mar | LE4 |
| KJ-LM-16 | 1115 | Lomas del Mar | 36 | 1 | 1 | Moin | Lomas del Mar | LE5 |
| KJ-LM-17 | 1116 | Lomas del Mar | 36 | 12 | 7 | Moin | Lomas del Mar | LE5 |
| KJ-LM-18 | 1117 | Lomas del Mar | 36 | 15 | 7 | Moin | Lomas del Mar | LE5 |
| KJ-LM-19 | 1118 | Lomas del Mar | 36 | 42 | 16 | Moin | Lomas del Mar | LE5 |
| KJ-LM-20 | 1119 | Lomas del Mar | 36 | 18 | 8 | Moin | Lomas del Mar | LE5 |
| KJ-LM-21 | 1120 | Lomas del Mar | 36 | 11 | 8 | Moin | Lomas del Mar | LE5 |
| KJ-LM-22 | 1121 | Lomas del Mar | 36 | 15 | 9 | Moin | Lomas del Mar | LE5 |
| KJ-LM-23 | 1122 | Lomas del Mar | 36 | 12 | 9 | Moin | Lomas del Mar | LE5 |
| KJ-LM-24 | 1123 | Lomas del Mar | 36 | 18 | 9 | Moin | Lomas del Mar | LE5 |
| KJ-LM-25 | 1971 | Lomas del Mar | 36 | 24 | 14 | Moin | Lomas del Mar | LE5 |
| KJ-LM-26 | 1972 | Lomas del Mar | 36 | 24 | 14 | Moin | Lomas del Mar | LE5 |
| CJ-92-06-07 | 948 | Lomas del Mar | 36 | 2 | 2 | Moin | Lomas del Mar | LE6 |
| CJ-92-06-08 | 949 | Lomas del Mar | 36 | 1 | 1 | Moin | Lomas del Mar | LE6 |

Table 1.—Continued.

| Field number | PPP number | Site name | Strat. section number | Number of specimens | Number of species | Formation | Reef trend | Locality code |
|---|---|---|---|---|---|---|---|---|
| KJ-LM-09 | 1108 | Lomas del Mar | 36 | 15 | 11 | Moin | Lomas del Mar | LE7 |
| KJ-LM-10 | 1109 | Lomas del Mar | 36 | 21 | 10 | Moin | Lomas del Mar | LE7 |
| KJ-LM-11 | 1110 | Lomas del Mar | 36 | 8 | 7 | Moin | Lomas del Mar | LE7 |
| KJ-LM-12 | 1111 | Lomas del Mar | 36 | 14 | 6 | Moin | Lomas del Mar | LE7 |
| KJ-LM-13 | 1112 | Lomas del Mar | 36 | 11 | 7 | Moin | Lomas del Mar | LE7 |
| KJ-LM-14 | 1113 | Lomas del Mar | 36 | 19 | 8 | Moin | Lomas del Mar | LE7 |
| KJ-LM-15 | 1114 | Lomas del Mar | 36 | 38 | 13 | Moin | Lomas del Mar | LE7 |
| CJ-92-06-01 | 942 | Lomas del Mar | 36 | 30 | 17 | Moin | Lomas del Mar | LE8 |
| CJ-92-06-02 | 943 | Lomas del Mar | 36 | 28 | 13 | Moin | Lomas del Mar | LE8 |
| KJ-LM-01 | 1100 | Lomas del Mar | 36 | 55 | 16 | Moin | Lomas del Mar | LE9 |
| KJ-LM-02 | 1101 | Lomas del Mar | 36 | 7 | 5 | Moin | Lomas del Mar | LE9 |
| KJ-LM-03 | 1102 | Lomas del Mar | 36 | 21 | 13 | Moin | Lomas del Mar | LE9 |
| KJ-LM-04 | 1103 | Lomas del Mar | 36 | 11 | 5 | Moin | Lomas del Mar | LE9 |
| KJ-LM-05 | 1104 | Lomas del Mar | 36 | 22 | 12 | Moin | Lomas del Mar | LE9 |
| KJ-LM-06 | 1105 | Lomas del Mar | 36 | 21 | 9 | Moin | Lomas del Mar | LE9 |
| KJ-LM-07 | 1106 | Lomas del Mar | 36 | 22 | 10 | Moin | Lomas del Mar | LE9 |
| KJ-LM-08 | 1107 | Lomas del Mar | 36 | 17 | 9 | Moin | Lomas del Mar | LE9 |
| AB93-71 | 1389 | Lomas del Mar | 36 | 63 | 24 | Moin | Lomas del Mar | LE10 |
| JW93-01 | 1412 | Lomas del Mar | 36 | 15 | 10 | Moin | Lomas del Mar | LE10 |
| JW93-02 | 1413 | Lomas del Mar | 36 | 14 | 10 | Moin | Lomas del Mar | LE10 |
| JW93-03 | 1414 | Lomas del Mar | 36 | 14 | 9 | Moin | Lomas del Mar | LE10 |
| JW93-04 | 1415 | Lomas del Mar | 36 | 19 | 14 | Moin | Lomas del Mar | LE10 |
| JW93-05 | 1416 | Lomas del Mar | 36 | 24 | 15 | Moin | Lomas del Mar | LE10 |
| JW93-06 | 2005 | Lomas del Mar | 36 | 18 | 14 | Moin | Lomas del Mar | LE10 |
| JW93-07 | 2006 | Lomas del Mar | 36 | 24 | 15 | Moin | Lomas del Mar | LE10 |
| JW93-08 | 2007 | Lomas del Mar | 36 | 6 | 6 | Moin | Lomas del Mar | LE10 |
| JW93-09 | 2008 | Lomas del Mar | 36 | 10 | 8 | Moin | Lomas del Mar | LE10 |
| JW93-10 | 2009 | Lomas del Mar | 36 | 15 | 12 | Moin | Lomas del Mar | LE10 |
| JW93-11 | 2010 | Lomas del Mar | 36 | 9 | 7 | Moin | Lomas del Mar | LE10 |
| JW93-12 | 2011 | Lomas del Mar | 36 | 21 | 11 | Moin | Lomas del Mar | LE10 |
| JW93-13 | 1385 | Lomas del Mar | 36 | 12 | 10 | Moin | Lomas del Mar | LE10 |
| JW93-14 | 1410 | Lomas del Mar | 36 | 11 | 8 | Moin | Lomas del Mar | LE10 |
| JW93-15 | 1309 | Lomas del Mar | 36 | 45 | 25 | Moin | Lomas del Mar | LE10 |
| AB93-65 | 1375 | Av. Barracuda–dorms | 38 | 7 | 5 | Moin | Lomas del Mar | LW1 |
| AB-93-21 | 1331 | Av. Barracuda | 38 | 16 | 12 | Moin | Lomas del Mar | LW2 |
| AB-93-22 | 1332 | Av. Barracuda | 38 | 33 | 15 | Moin | Lomas del Mar | LW2 |
| AB93-47 | 1357 | Av. Barracuda–dirt | 38 | 9 | 7 | Moin | Lomas del Mar | LW3 |
| AB93-48 | 1358 | Av. Barracuda–dirt | 38 | 13 | 10 | Moin | Lomas del Mar | LW3 |
| AB93-23 | 1333 | apt. complex | none | 19 | 13 | Moin | Lomas del Mar | P1 |
| AB93-24 | 1334 | apt. complex | none | 30 | 16 | Moin | Lomas del Mar | P1 |
| AB93-25 | 1335 | apt. complex | none | 22 | 15 | Moin | Lomas del Mar | P1 |
| AB93-26 | 1336 | apt. complex | none | 26 | 17 | Moin | Lomas del Mar | P1 |
| AB93-27 | 1337 | apt. complex | none | 14 | 11 | Moin | Lomas del Mar | P1 |
| AB93-28 | 1338 | apt. complex | none | 13 | 9 | Moin | Lomas del Mar | P1 |
| AB93-29 | 1339 | apt. complex | none | 5 | 4 | Moin | Lomas del Mar | P1 |
| AB93-72 | 1390 | apt. complex | none | 11 | 9 | Moin | Lomas del Mar | P1 |
| AB93-42 | 1352 | Portete | none | 6 | 6 | Moin | Lomas del Mar | P2 |
| AB93-43 | 1353 | Portete | none | 7 | 5 | Moin | Lomas del Mar | P2 |
| KJ-P1 | 1126 | Portete Reef #1 | none | 5 | 4 | Moin | Lomas del Mar | P2 |
| KJ-P2 | 1127 | Portete Reef #2 | none | 35 | 11 | Moin | Lomas del Mar | P2 |
| AB93-45 | 1355 | Bahia Portete | none | 4 | 4 | Moin | Lomas del Mar | P3 |

*Costa Rica:*

total no. collections = 107

total no. specimens = 2392

median no. specimens per collection = 15

min–max no. specimens per collection = 1–146

Table 1.—Continued.

| Field number | PPP number | Site name | Strat. section number | Number of specimens | Number of species | Formation | Reef trend | Locality code |
|---|---|---|---|---|---|---|---|---|
| total no. species = 87 | | | | | | | | |
| median no. species per collection = 10 | | | | | | | | |
| min–max no. species per collection = 1–31 | | | | | | | | |
| Panama: | | | | | | | | |
| AB93-74 | 1423 | Paunch | none | 27 | 13 | — | — | PA |
| AB93-75 | 1424 | Paunch | none | 5 | 5 | — | — | PA |
| AB93-76 | 2002 | Swan Cay | 25 | 6 | 6 | — | — | SC |
| AB93-77 | 1285 | Ground Creek–west | none | 6 | 2 | — | — | GC |
| AB93-79 | 1260 | Hill Point–south | 26 | 12 | 6 | — | — | HP |
| AB93-80 | 1425 | Hill Point–west | 26 | 18 | 14 | — | — | HP |
| CJ-93-20-02 | 943 | Isla Bastimentos | 22 | 20 | 10 | — | — | FH |
| *Panama:* | | | | | | | | |
| total no. collections = 7 | | | | | | | | |
| total no. specimens = 95 | | | | | | | | |
| median no. specimens per collection = 12 | | | | | | | | |
| min–max no. specimens per collection = 5–27 | | | | | | | | |
| total no. species = 36 | | | | | | | | |
| median no. species per collection = 6 | | | | | | | | |
| min–max no. species per collection = 2–14 | | | | | | | | |

have been a single colony) collected at a single site. A *'site'* is defined as a coral-rich horizon exposed at an outcrop on a particular day. *'Sites'* may vary in vertical and lateral dimensions. A *'collection'* is made at a *'site'*. Different site numbers are assigned if the same horizon at a given outcrop is recollected on different days. On the other hand, we use the term *'locality'* to mean a *group* of *'collections'* made within an area having precisely defined vertical and lateral dimensions. In the present work, the vertical dimension of a locality is defined as 3–5 m, and the lateral dimension as 300–500 m. Therefore, *'sites'* are designated in the field and assigned field numbers (and corresponding PPP numbers; see Kaufmann, this volume); whereas *'localities'* are defined subsequent to field work, with reference to specific maps and stratigraphic sections. Our usage of the term *'locality'* therefore differs from that in other fossil groups (*e.g.*, bryozoans) treated in this volume. Our *'localities'* are roughly equivalent to correlated site codes (CSC numbers) in the PPP Database (Kaufmann, this volume). Finally, we use the term *'assemblage'* to refer to the taxa collected at a given locality.

## LIST OF ASSOCIATED MAPS AND SECTIONS

The collection sites treated in this paper are shown on the following maps and columns in Appendices A and B. Unless otherwise indicated, citations to maps and sections in this paper refer only to those given on this list.

*Costa Rica:*

Appendix B, Section 33: Chocolate to Buenos Aires
Appendix B, Section 34: Empalme
Appendix B, Section 35: Pueblo Nuevo Cemetery
Appendix B, Section 36: Lomas del Mar, Eastern Sequence
Appendix B, Section 38: Lomas del Mar, Western Reef Track Sequence

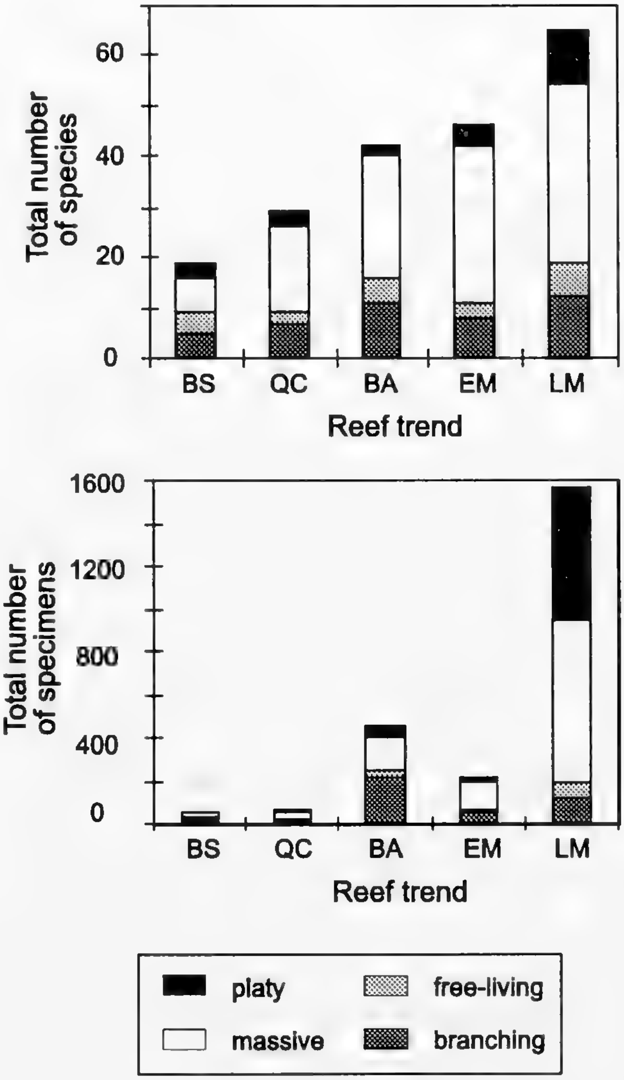
*Panama:*

Appendix B, Section 22: Isla Bastimentos, Fish Hole, Eastern Sequence
Appendix B, Section 25: Swan Cay, North of Isla Colon
Appendix B, Section 26: Isla Colon, Hill Point

## COLLECTING SITES AND LOCALITIES

Collections of hermatypic corals were made at a total of 107 sites within a 25 × 15 km area near Limon (Table 1; Appendix 1; Appendix A): one in the Brazo Seco patch (Rio Banano Formation), two in the Quebrada Chocolate trends (Quebrada Chocolate Formation), 21 in the Buenos Aires trend (Quebrada Chocolate Formation), 10 in the Empalme trend and associated Santa Rosa patch (Moin Formation), and 73 in the Lomas del Mar trend (Moin Formation). Detailed descriptions of the general geology of the Limon area and of particular reef trends are provided by Coates (this volume). Of importance to the present study, these descriptions indicate that the fossil reef corals that crop out in the five trends show evidence of only minor, local transport. At each site, some colonies were found upright and in place, and most show no signs of excessive breakage or wear. Furthermore, none of the collected horizons reveal strong internal stratification. Thus, throughout our assessment and analyses of the collections that follow, we assume that each of the collected coral assemblages consists largely of species that lived together in life.

To make the collections, individual coral specimens were extracted from the face of the outcrop using a rock hammer. Specimens were selected so that the collections would be *qualitatively* representative of the species composition of each site and their relative abundance. The species composition of each site was assessed by visually examining the exposure and distinguishing species without assigning names. Relative abundances of species were determined following a similar qualitative approach. Only specimens that appeared to be potentially identifiable to species were collected. In the Limon area, outcrops usually occur along recently bulldozed roads or construction sites and along creek banks, and are generally small in size (usually <5 m high, <15 m wide). Because of extreme variability in the amount, size, and preservation of coral specimens at different outcrops as well as in the objectives of different collectors; equivalent volumes of material were not collected at each site. Similarly, sizes of sites ranged from meter-square quadrats (*e.g.*, the 'KJ-LM' and 'JW' field numbers at Lomas del Mar east, see Table 1) to outcrops that were 5 × 15 m in dimension. Because of these inconsistencies, data from the collections cannot be analyzed statistically without grouping the collections into more uniform and meaningful sampling units.



Text-figure 2.—Bar charts showing the total numbers of species and specimens collected in the Limon reef trends. Bars are shaded according to four colony shape categories. The trends are arranged in chronological order from oldest (left) to youngest (right). BS, Brazo Seco patch; QC, Quebrada Chocolate trends; BA, Buenos Aires trend; EM, Empalme trend (including Santa Rosa patch); LM, Lomas del Mar trend.

Comparisons among reef trends (Text-fig. 2) show that many more specimens and species were collected overall in the Lomas del Mar trend, and fewer were collected in the Brazo Seco patch and Quebrada Chocolate trends. Because of exceptional preservation and abundance, collecting was especially intense in six coral-rich siltstone horizons (0.5–3 m thick) exposed at the southeast side of the Lomas del Mar trend (Appendices A; B, Section 36): two collections (PPP 639, 646; 163 specimens, 32 species) were made in 1989 in the two lowest horizons (Appendix B, Section 36: 32–34 m, 37–38 m); 32 collections (PPP 942–943, 948–949, 962–963, 1100–1123, 1971–1972; 772 specimens, 50 species) were made in 1992 in the middle three horizons (Appendix B, Section 36: 45–47 m, 49.5–50 m, 52.5–53 m); and 16 collections (PPP 1309, 1385, 1389, 1410, 1412–1416, 2005–2011; 320 specimens, 39 species) were made in 1993 in the upper horizon (Appendix B, Section 36: 61–64 m). A similar reef coral fauna, also exceptionally rich and well-preserved, was collected in 1995 on the south side near the middle of the Lomas del Mar trend (PPP 2037; Appendix B, Section 38), and is currently being washed and identified.

Collecting was more limited in the Buenos Aires and Empalme trends primarily because of poorer preservation. We surveyed numerous small exposures of these two trends, but the corals were often extensively recrystallized. Collecting efforts were most reduced in the Quebrada Chocolate trends and in the Brazo Seco patch, mainly because of lack of field time. Clearly, these older trends and other sites in the Santa Rita and Rio Blanco areas could prove essential to a more comprehensive documentation of Pliocene events preceding and concurrent with Plio-Pleistocene turnover in Caribbean reef communities and therefore warrant more thorough study in the future.

To ensure that localities were consistently defined in statistical analyses of the collections, all specimens collected within 300–500 m of one another laterally and 3–5 m of one another vertically were grouped together into localities (34 total) (Text-fig. 1; Tables 1, 2). These groupings were made by careful study of the 1:10000 Ciudad de Limon (Edicion 2—IGNCR 1989) and the 1:50000 Rio Banano (3545-I, Edicion 2—IGNCR 1989) and 1:50000 Moin (3546-II, Edicion 3—IGNCR 1989) topographic sheets and Appendix B, Sections 33, 34, 36, 38. Based on these groupings, only one locality was represented within the Brazo Seco patch, two in the Quebrada Chocolate trend, eight in the Buenos Aires trend, seven in the Empalme trend, and 16 in the Lomas del Mar trend (Text fig. 1; Table 1).

In general, numbers of specimens collected per locality range from two to 320 (median = 45), and numbers of species collected per locality range from one to 39 (median = 19.5). Study of the frequencies of numbers of species and specimens per locality suggests that a disproportionally high number of localities contain low numbers of species and specimens (Text-fig. 3). Ideally, if sampling were equal in different localities and the localities were equal in species richness, the two histograms in Text-figure 3 should be more or less bell-shaped; however, the distribution for number of species is platykurtic and the distribution for specimens is skewed to the right. Therefore, seven of the 34 localities with fewer than 10 specimens (those with double asterisks in Table 2) were dropped in subsequent statistical analyses, leaving a total of 27 localities in the analyzed data set. In addition, as shown in the scatterplot in Text-figure 3, the relationship between numbers of species per locality and number of specimens per locality changes sharply near a locality having 30 specimens and 18 species (BA3). Six additional localities that have fewer than 30 specimens were thus treated with caution in subsequent statistical analyses.

Results of Kruskal-Wallis Non-parametric One-way Analysis of Variance (using the 27 localities with > 16 specimens) indicate that no significant difference exists among trends in numbers of specimens (Corrected Chi-Square = 5.372, D.F. = 4, p-value = 0.251) or species (Corrected Chi-Square = 5.492, D.F. = 4, p-value = 0.240) collected per locality (Text-fig. 4). These results suggest that sampling intensity was roughly equivalent *within* localities in the different reef trends.

## TAXA

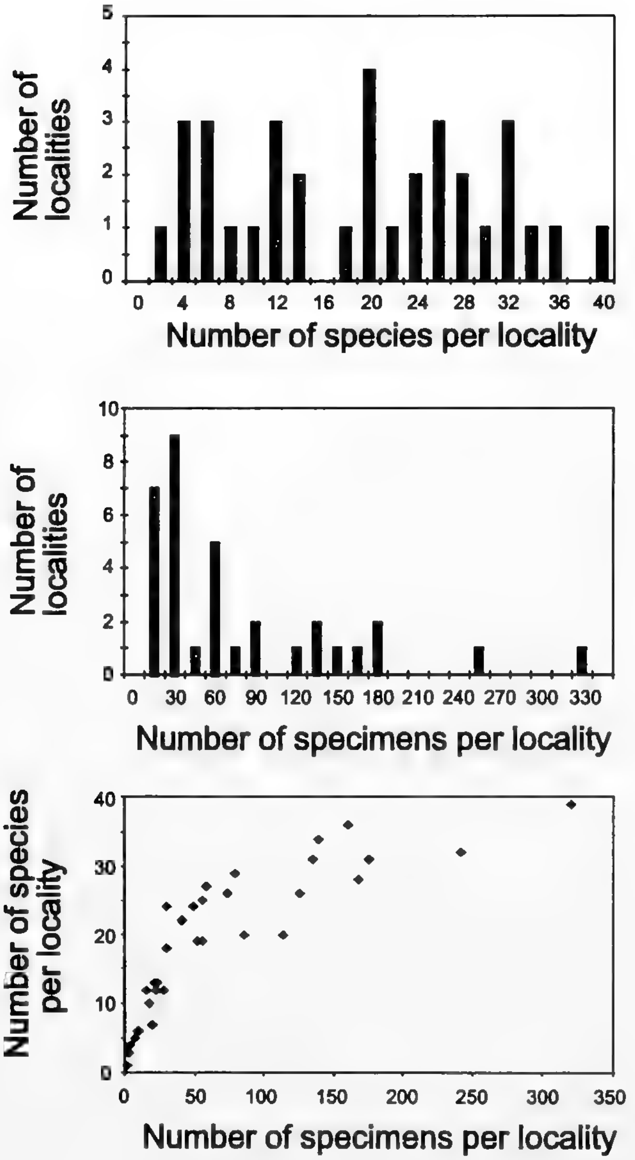
### IDENTIFICATION AND GENERAL DESCRIPTION

Budd and Stemann identified a total of 82 species belonging to 31 genera in the collections (Table 3). Five additional species were present, but could not be identified due to poor preservation. To guide us in making identifications, we used a consistent set of characters and character states developed on the basis of morphometric analyses of Neogene and Recent coral samples collected across the Caribbean region (Foster 1986, 1987; Foster *et al.,* 1988; Budd, 1991; Stemann, 1991, in press; Budd *et al.,* 1994a, b; Swedberg, 1994; Johnson and Budd, 1996; Budd and Johnson, 1999). Lists and illustrated definitions of these characters along with information on species authorship and synonyms are currently available on the World-Wide Web at http://nmita.geology.uiowa.edu. A specimen database (Appendix) is also available at the same address. As part of the identification procedure, we assigned identification confidence codes to each specimen as follows: 1 = 100% confident, 2 = 75% confident, 3 = 50% confident, 4 ≤ 25% confident.

The total number of species (87) recognized in the Costa Rican collections is less than the total number of species (107) estimated to have lived in the entire Caribbean region between 5.5 and 1.5 Ma, as documented in the 1996 Cenozoic Coral Database (CCD) compiled by Johnson and Budd in S-plus using STATPOD (Johnson and McCormick, 1995; Budd and Johnson, 1997). Nevertheless, cumulative number of species curves for the 27 better-sampled localities (Text-fig. 5) suggest that a major proportion of the species in the Limon reef trends has been sampled. These curves differ from more traditional species area curves used in ecology (Ricklefs, 1990) in that our localities do not represent repeated samples from a single statistical population. Instead, the localities are samples of a fauna that is undergoing change and therefore represent different stages in a faunal transition. Because they are not replicate samples, curves were constructed using two methods: (1) the localities were added in temporal order beginning with the stratigraphically oldest reef trend and continuing to the youngest (Text-fig. 5A), and (2) the data were randomly resampled to determine the average number of species as a function of numbers of localities sampled (PC-ORD, Version

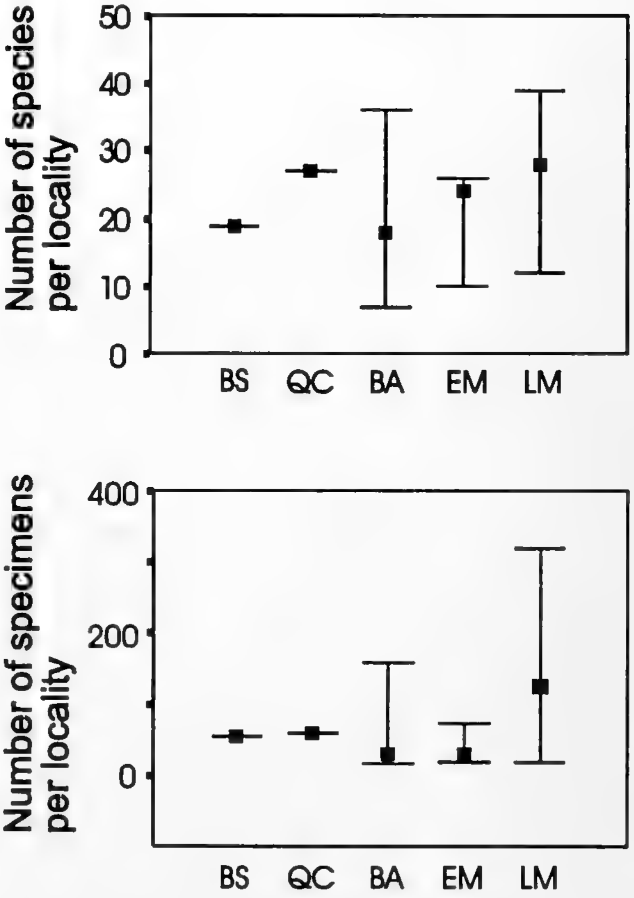
Table 2.—Numbers of identified specimens and species collected within localities and reef trends. Localities with double asterisks were not included in statistical analyses; localities with single asterisks were treated with caution.

| | | All | | Branching | | Freeliving | | Massive | | Platy | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Reef trend | Locality code | No. species | No. specimens | No. species | No. specimens | No. species | No. specimens | No. species | No. specimens | No. species | No. specimens |
| Brazo Seco | BS | 19 | 56 | 5 | 25 | 4 | 11 | 7 | 14 | 3 | 6 |
| *All localities* | *n = 1* | *19* | *56* | *5* | *25* | *4* | *11* | *7* | *14* | *3* | *6* |
| Q. Chocolate | C2** | 6 | 10 | 3 | 5 | 0 | 0 | 3 | 5 | 0 | 0 |
| Q. Chocolate | C4 | 27 | 59 | 7 | 14 | 2 | 4 | 15 | 31 | 3 | 10 |
| *All localities* | *n = 2* | *29* | *69* | *7* | *19* | *2* | *4* | *17* | *36* | *3* | *10* |
| Buenos Aires | BA1* | 7 | 20 | 3 | 14 | 0 | 0 | 3 | 4 | 1 | 2 |
| Buenos Aires | BA2 | 20 | 86 | 7 | 39 | 1 | 1 | 10 | 31 | 2 | 15 |
| Buenos Aires | BA3 | 18 | 30 | 9 | 18 | 1 | 1 | 6 | 8 | 2 | 3 |
| Buenos Aires | BA4* | 12 | 16 | 5 | 8 | 0 | 0 | 7 | 8 | 0 | 0 |
| Buenos Aires | BA5** | 1 | 2 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| Buenos Aires | BA6 | 20 | 114 | 7 | 61 | 2 | 13 | 9 | 23 | 2 | 17 |
| Buenos Aires | BA7 | 36 | 160 | 9 | 66 | 4 | 15 | 21 | 69 | 2 | 10 |
| Buenos Aires | BA8* | 13 | 21 | 4 | 9 | 0 | 0 | 8 | 11 | 1 | 1 |
| *All localities* | *n = 8* | *42* | *449* | *11* | *217* | *5* | *30* | *24* | *154* | *2* | *48* |
| *Median* | *n = 7* | *18* | *30* | *7* | *18* | *1* | *1* | *8* | *11* | *1* | *2* |
| *Minimum* | *n = 7* | *7* | *16* | *3* | *8* | *0* | *0* | *3* | *4* | *0* | *0* |
| *Maximum* | *n = 7* | *36* | *160* | *9* | *66* | *4* | *15* | *21* | *69* | *2* | *17* |
| Empalme | E1** | 6 | 9 | 1 | 1 | 0 | 0 | 4 | 6 | 1 | 2 |
| Empalme | E2** | 4 | 4 | 1 | 1 | 0 | 0 | 3 | 3 | 0 | 0 |
| Empalme | E3 | 10 | 18 | 1 | 1 | 0 | 0 | 9 | 17 | 0 | 0 |
| Santa Rosa | SR1 | 24 | 30 | 7 | 9 | 2 | 2 | 14 | 18 | 1 | 1 |
| Santa Rosa | SR2 | 26 | 74 | 7 | 25 | 2 | 4 | 16 | 39 | 1 | 6 |
| Santa Rosa | SR3 | 25 | 56 | 3 | 7 | 1 | 2 | 17 | 38 | 4 | 9 |
| Santa Rosa | SR4* | 13 | 23 | 3 | 8 | 0 | 0 | 10 | 15 | 0 | 0 |
| *All localities* | *n = 7* | *46* | *214* | *8* | *52* | *3* | *8* | *31* | *136* | *4* | *18* |
| *Median* | *n = 5* | *24* | *30* | *3* | *8* | *1* | *2* | *14* | *18* | *1* | *1* |
| *Minimum* | *n = 5* | *10* | *18* | *1* | *1* | *0* | *0* | *9* | *15* | *0* | *0* |
| *Maximum* | *n = 5* | *26* | *74* | *7* | *25* | *2* | *4* | *17* | *39* | *4* | *9* |
| Lomas del Mar | LE1 | 22 | 41 | 5 | 10 | 1 | 2 | 11 | 16 | 5 | 13 |
| Lomas del Mar | LE2 | 31 | 135 | 4 | 10 | 3 | 7 | 16 | 41 | 8 | 77 |
| Lomas del Mar | LE3* | 12 | 28 | 1 | 1 | 0 | 0 | 5 | 5 | 6 | 22 |
| Lomas del Mar | LE4 | 32 | 242 | 3 | 28 | 4 | 14 | 18 | 93 | 7 | 107 |
| Lomas del Mar | LE5 | 28 | 168 | 2 | 8 | 1 | 1 | 19 | 97 | 6 | 62 |
| Lomas del Mar | LE6** | 3 | 3 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 2 |
| Lomas del Mar | LE7 | 26 | 126 | 1 | 5 | 1 | 1 | 19 | 85 | 5 | 35 |
| Lomas del Mar | LE8 | 29 | 79 | 4 | 8 | 4 | 14 | 15 | 40 | 5 | 16 |
| Lomas del Mar | LE9 | 31 | 175 | 3 | 7 | 4 | 8 | 18 | 69 | 6 | 91 |
| Lomas del Mar | LE10 | 39 | 320 | 3 | 22 | 3 | 27 | 25 | 159 | 8 | 112 |
| Lomas del Mar | LW1** | 5 | 7 | 1 | 1 | 0 | 0 | 2 | 2 | 2 | 4 |
| Lomas del Mar | LW2 | 24 | 49 | 7 | 11 | 2 | 2 | 11 | 21 | 4 | 15 |
| Lomas del Mar | LW3* | 12 | 22 | 0 | 0 | 1 | 2 | 5 | 8 | 6 | 12 |
| Lomas del Mar | P1 | 34 | 139 | 3 | 8 | 1 | 1 | 22 | 100 | 8 | 30 |
| Lomas del Mar | P2 | 19 | 52 | 4 | 6 | 1 | 1 | 10 | 23 | 4 | 22 |
| Lomas del Mar | P3** | 4 | 4 | 1 | 1 | 0 | 0 | 3 | 3 | 0 | 0 |
| *All localities* | *n = 16* | *65* | *1590* | *12* | *123* | *7* | *67* | *35* | *758* | *11* | *619* |
| *Median* | *n = 13* | *29* | *126* | *3* | *8* | *1* | *2* | *16* | *41* | *6* | *30* |
| *Minimum* | *n = 13* | *12* | *19* | *0* | *0* | *0* | *0* | *5* | *5* | *4* | *12* |
| *Maximum* | *n = 13* | *52* | *320* | *7* | *28* | *4* | *27* | *25* | *159* | *8* | *112* |
| Panama | PA | 14 | 32 | 0 | 0 | 0 | 0 | 11 | 28 | 3 | 4 |
| Panama | SC** | 6 | 6 | 3 | 3 | 0 | 0 | 2 | 2 | 1 | 1 |
| Panama | GC** | 2 | 6 | 2 | 6 | 0 | 0 | 0 | 0 | 0 | 0 |
| Panama | HP | 18 | 29 | 5 | 10 | 1 | 1 | 10 | 14 | 2 | 4 |
| Panama | FH | 11 | 21 | 2 | 3 | 4 | 13 | 4 | 4 | 1 | 1 |
| *All localities* | *n = 5* | *35* | *94* | *10* | *22* | *5* | *14* | *17* | *48* | *3* | *10* |
| *Minimum* | *n = 3* | *11* | *21* | *0* | *0* | *0* | *0* | *4* | *4* | *1* | *1* |
| *Maximum* | *n = 3* | *18* | *32* | *5* | *10* | *4* | *13* | *11* | *28* | *3* | *4* |



Text-figure 3.—Histograms and scatterplot showing the numbers of species and specimens collected per locality.

2.0, McCune and Mefford, 1995; Text-fig. 5B). The first curve (Text-fig. 5A) levels off in a series of stepped plateaus. The steps appear to correspond with reef trends and are best developed for localities within the three younger trends. This result indicates that the species that lived within each reef trend are more or less adequately sampled. On the other hand, the second curve (Text-fig. 5B) levels off at between 10 to 15 localities, again indicating that the sampled localities adequately estimate species richness.



Text-figure 4.—Maxima, medians, and minima of numbers of species and specimens collected per locality within each of five reef trends. The trends are arranged in chronological order from oldest (left) to youngest (right). BS, Brazo Seco patch; QC, Quebrada Chocolate trends; BA, Buenos Aires trend; EM, Empalme trend (including Santa Rosa patch); LM, Lomas del Mar trend.

Of the 82 identified species, 49 are living, and 33 are extinct (Table 4). The 49 living species represent 81.7% of the 60 hermatypic species in the Caribbean today (Budd *et al.*, 1994a). Among the living species are all of the species that dominate modern Caribbean shallow and deep reef communities (Goreau, 1959; Goreau and Wells, 1967), including *Acropora palmata, A. cervicornis, Undaria agaricites* ( = *tenuifolia*), *Agaricia lamarcki, Siderastrea siderea, Porites astreoides, P. furcata, Diploria strigosa,* members of the *Montastraea annularis* complex, and *Colpophyllia natans.* Also included are exceptionally well-preserved specimens of the modern, typically deep forereef species described by Wells (1973) [*e.g.*, species of *Madracis, Agaricia, Mycetophyllia, Dichocoenia*] and *Porites colonensis.* Eight of the species identified in the collections, represented by 76 specimens, are undescribed, as are species in at least two species complexes (*Montastraea 'limbata',* 88 specimens; *M. 'cavernosa',* 39 specimens). Among the extinct corals are several species of *Stylophora* that are common or abundant through Plio-Pleistocene intervals of the Ba-

Table 3.—List of species identified in collections, arranged by country in taxonomic order. Phaceloid colony shapes are classified as branching; solitary coralla as massive.

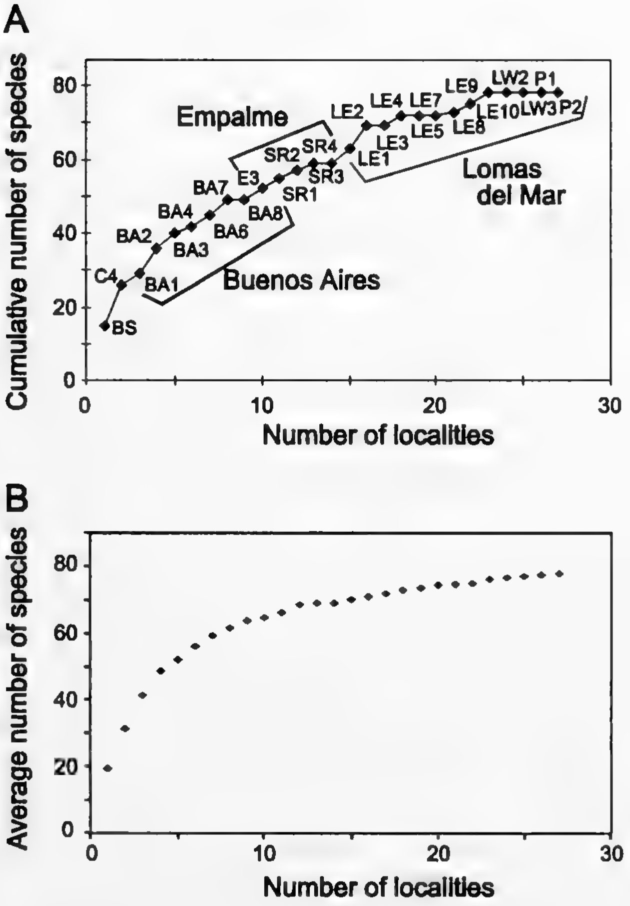
| Family | Genus | Species | CCD species ID no. | Colony shape | No. of specimens | No. of collections | No. of localities |
|---|---|---|---|---|---|---|---|
| *Costa Rica:* | | | | | | | |
| Astrocoeniidae | *Stephanocoenia* | *intersepta* | 2 | massive | 69 | 36 | 12 |
| Astrocoeniidae | *Stephanocoenia* | *duncani* | 3 | massive | 113 | 53 | 20 |
| Astrocoeniidae | *Stephanocoenia* | *spongiformis* | 4 | massive | 8 | 7 | 5 |
| Pocilloporidae | *Stylophora* | *affinis* | 5 | branching | 2 | 1 | 1 |
| Pocilloporidae | *Stylophora* | *granulata* | 7 | branching | 14 | 5 | 4 |
| Pocilloporidae | *Stylophora* | *minor* | 9 | branching | 7 | 3 | 3 |
| Pocilloporidae | *Stylophora* | *monticulosa* | 10 | branching | 8 | 7 | 6 |
| Pocilloporidae | *Pocillopora* | *crasssoramosa* | 15 | branching | 19 | 3 | 3 |
| Pocilloporidae | *Madracis* | *asperula* | 16.5 | branching | 26 | 18 | 5 |
| Pocilloporidae | *Madracis* | *decactis* | 17 | massive | 110 | 42 | 11 |
| Pocilloporidae | *Madracis* | *mirabilis* | 20 | branching | 55 | 24 | 11 |
| Pocilloporidae | *Madracis* | *pharensis* | 21 | massive | 1 | 1 | 1 |
| Pocilloporidae | *Madracis* | sp. A | 21.5 | branching | 2 | 1 | 1 |
| Acroporidae | *Acropora* | *cervicornis* | 22 | branching | 74 | 22 | 15 |
| Acroporidae | *Acropora* | *palmata* | 23 | branching | 45 | 21 | 14 |
| Agariciidae | *Agaricia* | *grahamae* | 29 | platy | 137 | 39 | 13 |
| Agariciidae | *Agaricia* | *lamarcki* | 30 | platy | 97 | 36 | 13 |
| Agariciidae | *Agaricia* | *undata* | 32 | platy | 67 | 32 | 12 |
| Agariciidae | *Undaria* | *agaricites* | 33 | platy | 324 | 79 | 25 |
| Agariciidae | *Undaria* | *crassa* | 34 | massive | 27 | 18 | 11 |
| Agariciidae | *Undaria* | *pusilla* | 35 | platy | 4 | 4 | 4 |
| Agariciidae | *Helioseris* | *cucullata* | 43 | platy | 27 | 19 | 14 |
| Siderastreidae | *Siderastrea* | *radians* | 56 | free-living | 3 | 2 | 2 |
| Siderastreidae | *Siderastrea* | *siderea* | 58 | massive | 42 | 28 | 20 |
| Poritidae | *Porites* | *astreoides* | 63 | massive | 52 | 30 | 17 |
| Poritidae | *Porites* | *portoricensis* | 65 | branching | 12 | 10 | 8 |
| Poritidae | *Porites* | *waylandi* | 68 | massive | 5 | 5 | 5 |
| Poritidae | *Porites* | *baracoaensis* | 69 | branching | 26 | 15 | 11 |
| Poritidae | *Porites* | *branneri* | 70 | massive | 18 | 14 | 10 |
| Poritidae | *Porites* | *colonensis* | 73 | massive | 14 | 9 | 4 |
| Poritidae | *Porites* | *furcata* | 76 | branching | 63 | 24 | 11 |
| Poritidae | *Porites* | *porites* | 77 | branching | 3 | 3 | 2 |
| Poritidae | *Goniopora* | *imperatoris* | 80 | massive | 1 | 1 | 1 |
| Faviidae | *Caulastraea* | *portoricensis* | 83 | branching | 58 | 26 | 17 |
| Faviidae | *Favia* | *fragum* | 88 | massive | 8 | 7 | 5 |
| Faviidae | *Diploria* | *clivosa* | 94 | massive | 12 | 7 | 7 |
| Faviidae | *Diploria* | *labyrinthiformis* | 95 | massive | 15 | 9 | 5 |
| Faviidae | *Diploria* | *sarasotana* | 96 | massive | 2 | 2 | 2 |
| Faviidae | *Diploria* | *strigosa* | 97 | massive | 38 | 24 | 19 |
| Faviidae | *Manicina* | *areolata* | 100 | free-living | 37 | 19 | 10 |
| Faviidae | *Manicina* | *mayori* | 101 | massive | 22 | 18 | 12 |
| Faviidae | *Manicina* | *puntagordensis* | 102 | free-living | 17 | 11 | 7 |
| Faviidae | *Thysanus* | sp. A | 109 | free-living | 19 | 11 | 7 |
| Faviidae | *Colpophyllia* | *amaranthus* | 112 | massive | 3 | 2 | 2 |
| Faviidae | *Colpophyllia* | *natans* | 114 | massive | 39 | 28 | 20 |
| Faviidae | *Colpophyllia* | sp. A | 114.5 | massive | 14 | 12 | 7 |
| Faviidae | *Montastraea* | *faveolata* | 117 | massive | 50 | 33 | 14 |
| Faviidae | *Montastraea* | *franksi* | 118 | massive | 34 | 19 | 11 |
| Faviidae | *Montastraea* | *limbata*-1 | 121.1 | massive | 10 | 6 | 5 |
| Faviidae | *Montastraea* | *limbata*-2 | 121.2 | massive | 77 | 38 | 21 |
| Faviidae | *Montastraea* | sp. A | 122 | massive | 29 | 16 | 11 |
| Faviidae | *Montastraea* | *canalis* | 124 | massive | 11 | 9 | 8 |
| Faviidae | *Montastraea* | *cavernosa*-2 | 126 | massive | 32 | 27 | 15 |
| Faviidae | *Montastraea* | *cavernosa*-3 | 127 | massive | 7 | 6 | 6 |
| Faviidae | *Montastraea* | *cylindrica* | 128 | massive | 113 | 44 | 14 |
| Faviidae | *Solenastrea* | *bournoni* | 131 | massive | 23 | 6 | 5 |

Table 3.—Continued.

| Family | Genus | Species | CCD species ID no. | Colony shape | No. of speci- mens | No. of collec- tions | No. of local- ities |
|---|---|---|---|---|---|---|---|
| Trachyphyllidae | *Antillophyllia* | *sawkinsi* | 137 | free-living | 2 | 2 | 2 |
| Meandrinidae | *Meandrina* | *braziliensis* | 138 | free-living | 1 | 1 | 1 |
| Meandrinidae | *Meandrina* | *meandrites* | 139 | massive | 9 | 9 | 6 |
| Meandrinidae | *Meandrina* | sp. A | 139.5 | massive | 7 | 5 | 3 |
| Meandrinidae | *Placocyathus* | *trinitatis* | 143 | free-living | 2 | 1 | 1 |
| Meandrinidae | *Placocyathus* | *variabilis* | 144 | free-living | 38 | 21 | 11 |
| Meandrinidae | *Dichocoenia* | *caloosahatcheensis* | 145 | massive | 1 | 1 | 1 |
| Meandrinidae | *Dichocoenia* | *eminens* | 146 | massive | 1 | 1 | 1 |
| Meandrinidae | *Dichocoenia* | *stokesi* | 148 | massive | 22 | 14 | 10 |
| Meandrinidae | *Dichocoenia* | *stellaris* | 149 | massive | 16 | 13 | 10 |
| Meandrinidae | *Dichocoenia* | *tuberosa* | 150 | massive | 6 | 5 | 4 |
| Oculinidae | *Archohelia* | *limonensis* | 152.5 | branching | 2 | 2 | 1 |
| Mussidae | *Antillia* | *dentata* | 153 | free-living | 1 | 1 | 1 |
| Mussidae | *Scolymia* | *cubensis* | 155 | massive | 8 | 5 | 3 |
| Mussidae | *Scolymia* | *lacera* | 157 | massive | 2 | 2 | 2 |
| Mussidae | *Mussa* | *angulosa* | 158 | branching | 12 | 9 | 7 |
| Mussidae | *Mussismilia* | aff. *M. hartti* | 160.5 | branching | 12 | 6 | 5 |
| Mussidae | *Isophyllastrea* | sp. B | 164.5 | massive | 1 | 1 | 1 |
| Mussidae | *Mycetophyllia* | *aliciae* | 166 | platy | 2 | 2 | 2 |
| Mussidae | *Mycetophyllia* | *danaana* | 168 | massive | 15 | 11 | 6 |
| Mussidae | *Mycetophyllia* | *ferox* | 169 | platy | 13 | 11 | 7 |
| Mussidae | *Mycetophyllia* | *lamarckiana* | 170 | platy | 5 | 5 | 5 |
| Mussidae | *Mycetophyllia* | *reesi* | 171 | platy | 22 | 15 | 8 |
| Mussidae | *Mycetophyllia* | sp. A | 171.5 | platy | 3 | 2 | 2 |
| Caryophylliidae | *Eusmilia* | *fastigiata* | 173 | branching | 7 | 6 | 4 |
| Caryophylliidae | *Eusmilia* | sp. A | 175 | branching | 1 | 1 | 1 |
| Costa Rica: | total no. genera = | 31 | | | | | |
| | total no. species = | 82 | | | | | |
| | total no. specimens | 2356 | | | | | |
| *Panama:* | | | | | | | |
| Astrocoeniidae | *Stephanocoenia* | *duncani* | 3 | massive | 2 | 2 | 2 |
| Pocilloporidae | *Stylophora* | *affinis* | 5 | branching | 1 | 1 | 1 |
| Pocilloporidae | *Stylophora* | *granulata* | 7 | branching | 4 | 1 | 1 |
| Pocilloporidae | *Stylophora* | *monticulosa* | 10 | branching | 2 | 1 | 1 |
| Pocilloporidae | *Pocillopora* | *crassoramosa* | 15 | branching | 1 | 1 | 1 |
| Pocilloporidae | *Madracis* | *asperula* | 16.5 | branching | 1 | 1 | 1 |
| Pocilloporidae | *Madracis* | *decactis* | 17 | massive | 1 | 1 | 1 |
| Acroporidae | *Acropora* | *cervicornis* | 22 | branching | 1 | 1 | 1 |
| Acroporidae | *Acropora* | *palmata* | 23 | branching | 2 | 2 | 2 |
| Agariciidae | *Undaria* | *agaricites* | 33 | platy | 7 | 5 | 4 |
| Agariciidae | *Undaria* | *crassa* | 34 | massive | 1 | 1 | 1 |
| Agariciidae | *Helioseris* | *cucullata* | 43 | platy | 2 | 2 | 2 |
| Siderastreidae | *Siderastrea* | *siderea* | 58 | massive | 3 | 3 | 2 |
| Poritidae | *Porites* | *astreoides* | 63 | massive | 2 | 2 | 2 |
| Poritidae | *Porites* | *baracoaensis* | 69 | branching | 5 | 1 | 1 |
| Poritidae | *Porites* | *furcata* | 76 | branching | 1 | 1 | 1 |
| Faviidae | *Caulastraea* | *portoricensis* | 83 | branching | 4 | 2 | 2 |
| Faviidae | *Diploria* | *labyrinthiformis* | 95 | massive | 3 | 3 | 2 |
| Faviidae | *Diploria* | *strigosa* | 97 | massive | 7 | 3 | 2 |
| Faviidae | *Manicina* | *areolata* | 100 | free-living | 1 | 1 | 1 |
| Faviidae | *Manicina* | *puntagordensis* | 102 | free-living | 1 | 1 | 1 |
| Faviidae | *Thysanus* | *corbicula* | 111 | free-living | 1 | 1 | 1 |
| Faviidae | *Colpophyllia* | *natans* | 114 | massive | 6 | 2 | 2 |
| Faviidae | *Colpophyllia* | sp. A | 114.5 | massive | 5 | 2 | 2 |
| Faviidae | *Montastraea* | *faveolata* | 117 | massive | 6 | 4 | 3 |
| Faviidae | *Montastraea* | *franksi* | 118 | massive | 1 | 1 | 1 |
| Faviidae | *Montastraea* | *limbata*-2 | 121.2 | massive | 1 | 1 | 1 |
| Faviidae | *Montastraea* | *cavernosa*-2 | 126 | massive | 1 | 1 | 1 |

Table 3.—Continued.

| Family | Genus | Species | CCD species ID no. | Colony shape | No. of specimens | No. of collections | No. of localities |
|---|---|---|---|---|---|---|---|
| Meandrinidae | *Meandrina* | *braziliensis* | 138 | free-living | 3 | 1 | 1 |
| Meandrinidae | *Meandrina* | *meandrites* | 139 | massive | 1 | 1 | 1 |
| Meandrinidae | *Meandrina* | sp. A | 139.5 | massive | 5 | 2 | 2 |
| Meandrinidae | *Placocyathus* | *variabilis* | 144 | free-living | 8 | 1 | 1 |
| Meandrinidae | *Dichocoenia* | *eminens* | 146 | massive | 1 | 1 | 1 |
| Mussidae | *Mycetophyllia* | *danaana* | 168 | massive | 2 | 1 | 1 |
| Mussidae | *Mycetophyllia* | *ferox* | 169 | platy | 1 | 1 | 1 |
| Panama: | total no. genera = | 19 | | | | | |
| | total no. species = | 35 | | | | | |
| | total no. specimens | 94 | | | | | |



Text-figure 5.—Cumulative number of species curves assessing sampling adequacy. (A) Curve constructed by adding localities in stratigraphic order beginning with the oldest and continuing to the youngest. Each point represents a locality, the abbreviations for which are given in Table 1. The curve levels off in a series of steps corresponding to the different reef trends. (B) Curve constructed by randomly resampling localities. See text for details.

hamas Drilling Project cores (Budd and Kievman, in press).

Only five of the identified species are known only from the Limon area of Costa Rica (Table 4); therefore, most species (77 of 82) appear to have been widely distributed geographically. However, study of the numbers of localities and specimens per species shows that most species occur at relatively few localities and are represented by relatively few specimens (Text-fig. 6). A regression analysis of these two variables (y-intercept = −13.595, regression coefficient = 5.509) yields an adjusted R-square of 0.5127 and a p-value $<0.001$. Thus, most species are less common or rare within localities, and species with lower abundances tend to occur at fewer localities.

## ENVIRONMENTAL SIGNIFICANCE OF THE COLLECTED TAXA

Hermatypic coral assemblages are commonly used in sedimentology and stratigraphy to interpret ancient depositional environments (*e.g.*, James, 1984; Scoffin, 1987). They are especially important in shallow carbonate environments where environmentally diagnostic microfossils are rare. For example, comparisons between corals and lithologic data in lithostratigraphic units in the Bahamas Drilling Project cores show that interpretations based on corals correspond well with those based on independent sedimentologic criteria (Budd and Kievman, in press). Three characteristics of coral assemblages are examined in making these interpretations: (1) frequencies of different colony shapes, (2) species richness, and (3) occurrences of indicator species.

Following Geister (1983) and Graus and Macintyre (1989), an abundance of species with plate-shaped colonies can be interpreted to indicate deep forereef or low light environments. Mound-shaped or encrusting colonies indicate shallow platform or backreef conditions with high wave action. Mound-shaped and

Table 4.—Occurrences in the Limon reef trends. Species with asterisks are known only from the Limon area. Species identified with low confidences are indicated by question marks, and not included in ranges.

| Species | | CCD species ID number | Brazo Seco (5.3–4 Ma) | Q. Chocolate (3.6–3 Ma) | Buenos Aires (3.6–3 Ma) | Empalme (1.9–1.6 Ma) | Lomas del Mar (1.9–1.6 Ma) | Global first occurrence (FO) | Global last occurrence (LO) | Global age range (Ma) |
|---|---|---|---|---|---|---|---|---|---|---|
| *Stephanocoenia* | *intersepta* | 2 | | | | x | x | Pinecrest Ss, Florida (3.5–3 Ma) | Recent | 3.5–0 |
| *Stephanocoenia* | *duncani* | 3 | | x | x | x | x (LO) | Anguilla Fm, Anguilla (22–16.2 Ma) | | 22–1.6 |
| *Stephanocoenia* | *spongiformis* | 4 | | | | | x (LO) | Gurabo Fm, Dom. Rep. (7.5–5.6 Ma) | | 7.5–1.6 |
| *Stylophora* | *affinis* | 5 | | x | | | | Emperador Lm, Panama (22–17.6 Ma) | La Cruz Fm, Cuba (3.5–1.6 Ma) | 22–1.6 |
| *Stylophora* | *granulata* | 7 | | | x | | | Emperador Lm, Panama (22–17.6 Ma) | Unda-2, Bahamas (1.8–1.7 Ma) | 22–1.7 |
| *Stylophora* | *minor* | 9 | x | x | x | | | Tampa Fm, Florida (23.7–22 Ma) | Unda-3, Bahamas (1.9–1.8 Ma) | 23.7–1.8 |
| *Stylophora* | *monticulosa* | 10 | x | x | x | | | Baitoa Fm, Dom. Rep. (17.3–13.1 Ma) | Unda-2, Bahamas (1.8–1.7 Ma) | 17.3–1.7 |
| *Pocillopora* | *crassoramosa* | 15 | x | x | | | | Baitoa Fm, Dom. Rep. (17.3–13.1 Ma) | Old Pera Beds, Jamaica (2.5–1.8 Ma) | 17.3–1.8 |
| *Madracis* | *asperula* | 16.5 | | | | | x (FO) | | Recent | 1.9–0 |
| *Madracis* | *decactis* | 17 | x | | | x | x | Gurabo Fm, Dom. Rep. (8.3–7.5 Ma) | Recent | 8.3–0 |
| *Madracis* | *mirabilis* | 20 | | | | x | x | Tamana Fm, Trinidad (15–11.2 Ma) | Recent | 15–0 |
| *Madracis* | *pharensis* | 21 | | | | | x (FO) | | Recent | 1.9–0 |
| *Madricis* | sp. A(*) | 21.5 | x (FO, LO) | | | | | | | 5.3–4 |
| *Acropora* | *cervicornis* | 22 | | x (FO) | x | x | x | | Recent | 3.6–0 |
| *Acropora* | *palmata* | 23 | | | x (FO) | x | x | | Recent | 3.6–0 |
| *Agaricia* | *grahamae* | 29 | | | | | x (FO) | | Recent | 1.9–0 |
| *Agaricia* | *lamarcki* | 30 | | ? | | | x | Cercado Fm, Dom. Rep. (8.3–7.5 Ma) | Recent | 8.3–0 |
| *Agaricia* | *undata* | 32 | | | | | x | Gurabo Fm, Dom. Rep. (7.5–5.6 Ma) | Recent | 7.5–0 |
| *Undaria* | *agaricites* | 33 | ? | x | x | x | x | Cercado Fm, Dom. Rep. (8.3–7.5 Ma) | Recent | 8.3–0 |
| *Undaria* | *crassa* | 34 | x | x | x | x | x | Cercado Fm, Dom. Rep. (8.3–7.5 Ma) | Recent | 8.3–0 |
| *Undaria* | *pusilla* | 35 | x (FO) | | | x | x | | Recent | 5.3–0 |
| *Helioseris* | *cucullata* | 43 | x (FO) | x | x | | x | | Recent | 5.3–0 |
| *Siderastrea* | *radians* | 56 | | | x (FO) | | x | Pinecrest Ss, Florida (3.5–3 Ma) | Recent | 3.6–0 |
| *Siderastrea* | *siderea* | 58 | ? | x | x | x | x | Baitoa Fm, Dom. Rep. (17.3–13.1 Ma) | Recent | 3.6–0 |

Table 4.—Continued.

| Species | | CCD species ID number | Brazo Seco (5.3–4 Ma) | Q. Chocolate (3.6–3 Ma) | Buenos Aires (3.6–3 Ma) | Empalme (1.9–1.6 Ma) | Lomas del Mar (1.9–1.6 Ma) | Global first occurrence (FO) | Global last occurrence (LO) | Global age range (Ma) |
|---|---|---|---|---|---|---|---|---|---|---|
| *Porites* | *astreoides* | 63 | | ? | x (FO) | x | x | Pinecrest Ss, Florida (3.5–3 Ma) | Recent | 3.6–0 |
| *Porites* | *portoricensis* | 65 | | x | x | | x (LO) | Tampa Fm, Florida (23.7–22 Ma) | | 23.7–1.6 |
| *Porites* | *waylandi* | 68 | | ? | | | x (LO) | Tampa Fm, Florida (23.7–22 Ma) | | 23.7–1.6 |
| *Porites* | *baracoaensis* | 69 | x | x | x | | x (LO) | Emperador Lm, Panama (22–17.6 Ma) | Unda-2, Bahamas (1.8–1.7 Ma) | 22–0 |
| *Porites* | *branneri* | 70 | | | | ? | x | Pinecrest Ss, Florida (3.5–3 Ma) | Recent | 3.5–0 |
| *Porites* | *colonensis* | 73 | | | | | x (FO) | | Recent | 1.9–0 |
| *Porites* | *furcata* | 76 | | | x (FO) | x | x | | Recent | 3.6–0 |
| *Porites* | *porites* | 77 | | | x (FO) | x | | Pinecrest Ss, Florida (3.5–3 Ma) | Recent | 3.6–0 |
| *Goniopora* | *imperatoris* | 80 | | x | | | | Tampa Fm, Florida (23.7–22 Ma) | Unda-3, Bahamas (1.9–1.8 Ma) | 23.7–1.6 |
| *Caulastraea* | *portoricensis* | 83 | | | x | x | x (LO) | Lirio Lm, Mona (11.2–5.3 Ma) | Manchioneal Fm, Jamaica (1.8–1 Ma) | 11.2–1 |
| *Favia* | *fragum* | 88 | | x (FO) | x | | | Pinecrest Ss, Florida (3.5–3 Ma) | Recent | 3.5–0 |
| *Diploria* | *clivosa* | 94 | x (FO) | | x | x | | | Recent | 5.3 |
| *Diploria* | *labryinthiformis* | 95 | | | x (FO) | x | x | | Recent | 3.6–0 |
| *Diploria* | *sarasotana* | 96 | | | ? | ? | | Pinecrest Ss, Florida (3.5–3 Ma) | Pinecrest Ss, Florida (3.5–3 Ma) | 3.5–3 |
| *Diploria* | *strigosa* | 97 | | | x (FO) | x | x | Pinecrest Ss, Florida (3.5–3 Ma) | Recent | 3.6–0 |
| *Manicina* | *areolata* | 100 | | | x (FO) | x | x | Pinecrest Ss, Florida (3.5–3 Ma) | Recent | 3.6–0 |
| *Manicina* | *mayori* | 101 | | ? | x (FO) | x | x | | Recent | 3.6–0 |
| *Manicina* | *puntagordensis* | 102 | ? | | x (FO) | | x (LO) | | Caloosahatchee Fm, Florida (1.8–1.6 Ma) | 3.6–1.6 |
| *Thysanus* | sp. A | 109 | | x (FO) | x | x | x (LO) | | | 3.6–1.6 |
| *Colpophyllia* | *amaranthus* | 112 | | | x (FO) | x | | | Recent | 3.6–0 |
| *Colpophyllia* | *natans* | 114 | | ? | x | x | x | Gurabo Fm, Dom. Rep. (5.6–4.5 Ma) | Recent | 5.6–0 |
| *Colpophyllia* | sp. A | 114.5 | | | x (FO) | x | x | | Recent | 3.6–0 |
| *Montastraea* | *faveolata* | 117 | | | x (FO) | x | x | | Recent | 3.6–0 |
| *Montastraea* | *franksi* | 118 | | ? | x (FO) | x | x | | Recent | 3.6–0 |
| *Montastraea* | *limbata*-1 | 121.1 | | | x | x | x (LO) | ?Tamana Fm, Trinidad (15–11.2 Ma) | | 15–1.6 |

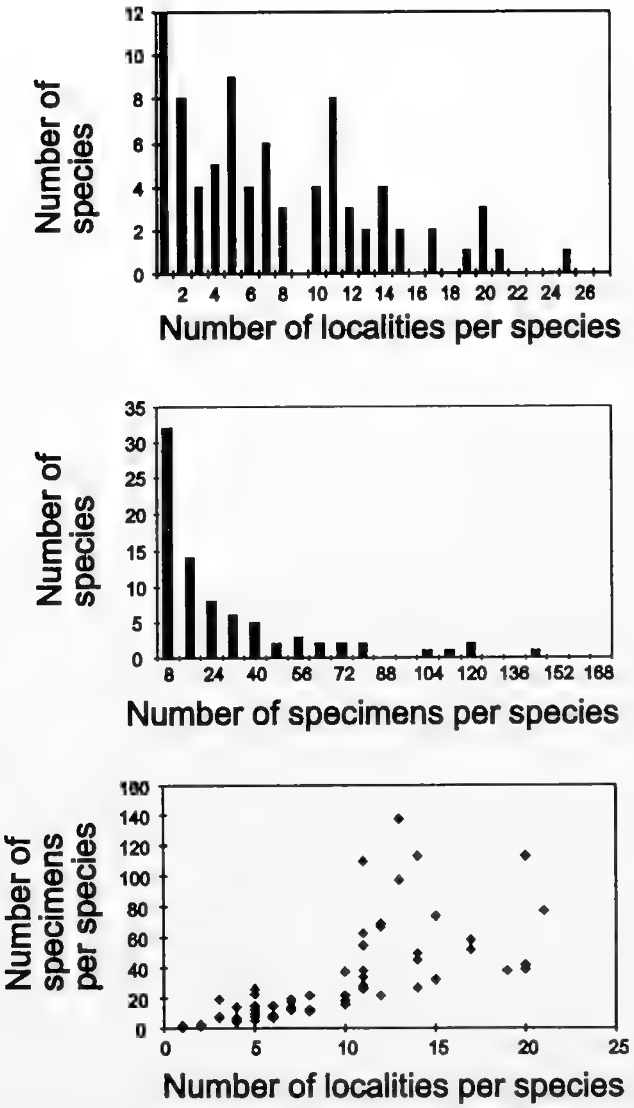
Table 4.—Continued.

| Species | | CCD species ID number | Brazo Seco (5.3–4 Ma) | Q. Chocolate (3.6–3 Ma) | Buenos Aires (3.6–3 Ma) | Empalme (1.9–1.6 Ma) | Lomas del Mar (1.9–1.6 Ma) | Global first occurrence (FO) | Global last occurrence (LO) | Global age range (Ma) |
|---|---|---|---|---|---|---|---|---|---|---|
| *Montastraea* | *limbata*-2 | 121.2 | | x | x | x | x (LO) | ?Tamana Fm, Trinidad (15–11.2 Ma) | | 15–1.6 |
| *Montastraea* | sp. A (*) | 122 | x (FO) | ? | x | x | x (LO) | | | 5.3–1.6 |
| *Montastraea* | *canalis* | 124 | | | ? | x | x (LO) | Tampa Fm, Florida (23.7–22 Ma) | | 23.7–1.6 |
| *Montastraea* | *cavernosa*-2 | 126 | | x | x | x | x | Baitoa Fm, Dom. Rep. (17.3–13.1 Ma) | Recent | 17.3–0 |
| *Montastraea* | *cavernosa*-3 | 127 | | | | x (FO) | x | | Recent | 1.9–0 |
| *Montastraea* | *cylindrica* | 128 | | | | x | x (LO) | Tamana Fm, Trinidad (15–11.2 Ma) | | 15–1.6 |
| *Solenastrea* | *bournoni* | 131 | x | x | | x | x | Tampa Fm, Florida (23.7–22 Ma) | Recent | 23.7–0 |
| *Antillophyllia* | *sawkinsi* | 137 | | | | | x (LO) | Anguilla Fm, Anguilla (22–16.2 Ma) | | 22–1.6 |
| *Meandrina* | *braziliensis* | 138 | ? | | | | | Cercado Fm, Dom. Rep. (8.3–7.5 Ma) | Recent | 8.3–0 |
| *Meandrina* | *meandrites* | 139 | | | | x | x | Pinecrest Ss, Florida (3.5–3 Ma) | Recent | 3.5–0 |
| *Meandrina* | sp. A | 139.5 | | | | ? | x | Gurabo Fm, Dom. Rep. (5.6–4.5 Ma) | Recent | 5.6–0 |
| *Placocyathus* | *trinitatis* | 143 | x | | | | | Manzanilla Fm, Trinidad (11.2–5.3 Ma) | Bowden Fm, Jamaica (3–2 Ma) | 11.2–2 |
| *Placocyathus* | *variabilis* | 144 | x | x | ? | ? | x (LO) | Baitoa Fm, Dom. Rep. (17.3–13.1 Ma) | | 17.3–1.6 |
| *Dichocoenia* | *caloosahatcheensis* | 145 | | | | x (LO) | | Mao Fm, Dom. Rep. (3.7–3.4 Ma) | Caloosahatchee Fm, Florida (1.8–1.6 Ma) | 3.7–1.6 |
| *Dichocoenia* | *eminens* | 146 | | x (FO) | | | | Pinecrest Ss, Florida (3.5–3 Ma | Caloosahatchee Fm, Florida (1.8–1.6 Ma) | 3.6–1.6 |
| *Dichocoenia* | *stokesi* | 148 | | ? | x (FO) | x | x | | Recent | 3.6–0 |
| *Dichocoenia* | *stellaris* | 149 | | | | x (FO) | x | | Recent | 1.9–0 |
| *Dichocoenia* | *tuberosa* | 150 | x | x | x | | x (LO) | Gurabo Fm, Dom. Rep. (7.5–5.6 Ma) | | 7.5–1.6 |
| *Archohelia* | *limonensis*(*) | 152.5 | | | | | x (FO, LO) | | | 1.9–1.6 |
| *Antillia* | *dentata* | 153 | | | | | ? | Cercado Fm, Dom. Rep. (8.3–7.5 Ma) | ?Gurabo Fm, Dom. Rep. (4.5–4 Ma) | 8.3–4 |
| *Scolymia* | *cubensis* | 155 | | | | | x | Gurabo Fm, Dom. Rep. (7.5–5.6 Ma) | Recent | 7.5–0 |
| *Scolymia* | *lacera* | 157 | | | | | x (FO) | | Recent | 1.9–0 |

Table 4.—Continued.

| Species | | CCD species ID number | Brazo Seco (5.3–4 Ma) | Q. Chocolate (3.6–3 Ma) | Buenos Aires (3.6–3 Ma) | Empalme (1.9–1.6 Ma) | Lomas del Mar (1.9–1.6 Ma) | Global first occurrence (FO) | Global last occurrence (LO) | Global age range (Ma) |
|---|---|---|---|---|---|---|---|---|---|---|
| *Mussa* | *angulosa* | 158 | | | x | x | x | Gurabo Fm, Dom. Rep. (7.5–5.6 Ma) | Recent | 7.5–0 |
| *Mussismilia* | aff. *M. hartti* | 160.5 | | | x | x | x (LO) | Gurabo Fm, Dom. Rep. (7.5–5.6 Ma) | | 7.5–1.6 |
| *Isophyllastrea* | sp. B(*) | 164.5 | | | x (FO, LO) | | | | | 3.6–3 |
| *Mycetophyllia* | *aliciae* | 166 | | | | | x (FO) | | Recent | 1.9–0 |
| *Mycetophyllia* | *danaana* | 168 | | | | | x (FO) | | Recent | 1.9–0 |
| *Mycetophyllia* | *ferox* | 169 | | | | x (FO) | x | | Recent | 1.9–0 |
| *Mycetophyllia* | *lamarckiana* | 170 | | | | ? | x (FO) | | Recent | 1.9–0 |
| *Mycetophyllia* | *reesi* | 171 | | | | | x (FO) | | Recent | 1.9–0 |
| *Mycetophyllia* | sp. A(*) | 171.5 | | | | | x (FO, LO) | | | 1.9–1.6 |
| *Eusmilia* | *fastigiata* | 173 | | | | x | x | Pinecrest Ss, Florida (3.5–3 Ma) | Recent | 3.5–0 |
| *Eusmilia* | sp. A | 175 | | ? | | | x (LO) | Gurabo Fm, Dom. Rep. (7.5–5.6 Ma) | | 7.5–1.6 |
| | Total number of species identified | | 15 | 21 | 39 | 41 | 64 | | | |
| | % living species | | 40 | 38.1 | 61.5 | 75.6 | 68.8 | | | |
| | Total number of first occurrences | | 5 | 4 | 16 | 3 | 11 | | | |
| | Total number of last occurrences | | 1 | 0 | 0 | 1 | 20 | | | |

Sources: Bahamas = Budd and Kievman (in press); Curaçao = Budd *et al.* (1998); Dominican Republic = Saunders *et al.* (1986); Jamaica = Budd and McNeill (1998); others = Budd *et al.* (1986) and Budd and Johnson (1997).



Text-figure 6.—Histograms and scatterplot showing the numbers of localities and specimens collected per species.

branching colonies indicate intermediate depths with moderate wave action on exposed forereefs. Exclusively branching species indicate muddy conditions with reduced wave action. Abundant free-living colonies indicate unstable substrates, often associated with seagrass flats. Following Done (1983) and Geister (1983), high diversities can be interpreted to indicate moderately exposed forereef environments at shallow to intermediate depths (5–20 m) on open marine leeward platforms; whereas low diversities indicate protected environments, such as shallow (<5 m) platform or deepest (40–100 m) shelf areas, or highly exposed (<5 m) windward reefs.

Recent species with narrow depth ranges (Goreau and Wells, 1967) that were identified in our collections include three shallow (<10 m) reef crest species (*Acropora palmata, Diploria strigosa, Colpophyllia amaranthus*) and four deeper (>20 m) forereef species (*Agaricia lamarcki, Mussa angulosa, Stephanocoenia intersepta, Madracis decactis*). Of these, *Diploria strigosa* may also occur at intermediate (10–20 m) depths, and the four deeper forereef species may also occur at shallower depths under turbid conditions. Therefore, the presences of indicator species should be interpreted with caution. Of the shallow reef crest indicators, *Acropora palmata* is perhaps the most definitive (see McNeill *et al.*, 1997).

To evaluate colony shapes of the collected corals, each species identified in the collections was assigned to one of four colony shape categories (Table 3), and percentages of species with different shapes at each locality were compared among reef trends. Following Johnson *et al.* (1995), the four categories consist of: branching (19 species, 439 specimens), free-living (10 species, 133 specimens), massive and encrusting (43 species, 1100 specimens) [hereafter termed 'massive'], and platy (11 species, 702 specimens). Species exhibiting more than one colony shape were assigned to the colony shape category that they most frequently possess.

Comparisons among trends indicate that species and specimens of platy corals are more frequent in localities in the Lomas del Mar trend; branching corals are more frequent in the Buenos Aires trend; and massive corals are more frequent in the Empalme trend (Table 5; Text-fig. 7). In general, corals in the less-collected older trends (the Brazo Seco patch and Quebrada Chocolate trend) appear to have colony shapes most like the Buenos Aires trend, although free-living corals are more common in the Brazo Seco patch (Text-fig. 7).

The differences in colony shapes among trends suggest that environmental conditions may have differed among trends. However, the high numbers of species collected in most localities suggest that most assemblages formed in exposed reef environments at shallow to intermediate depths (<30 m). The high percentages of platy corals in the Lomas del Mar trend suggest low light intensities, and thus either deep reef (30–40 m)

→

Text-figure 7.—Maxima, medians, and minima of percentages of species with branching, free-living, massive, and platy colony shapes within each of five reef trends. The trends are arranged in chronological order from oldest (left) to youngest (right). BS, Brazo Seco patch; QC, Quebrada Chocolate trends; BA, Buenos Aires trend; EM, Empalme trend (including Santa Rosa patch); LM, Lomas del Mar trend.

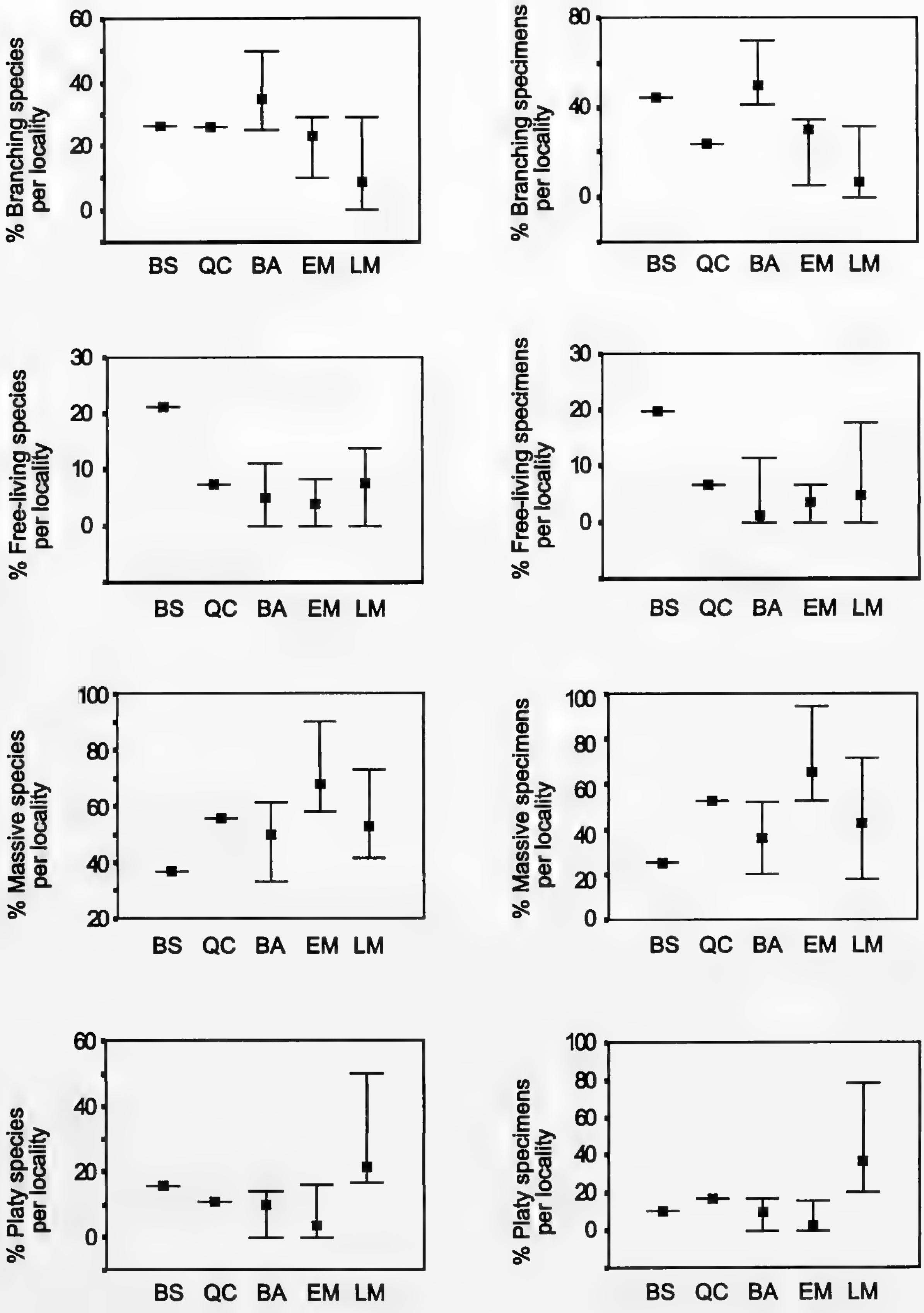
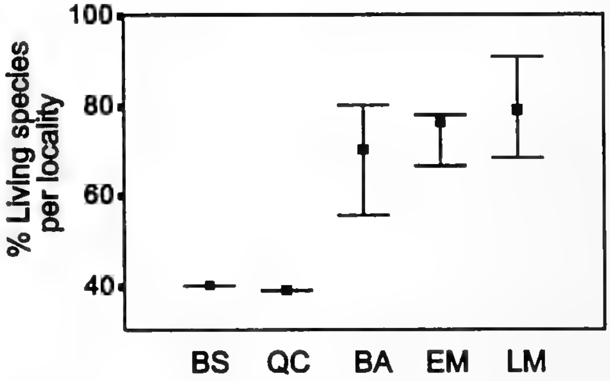

% Branching species per locality
60
40
20
0
BS QC BA EM LM
% Branching specimens per locality
80
40
0
BS QC BA EM LM
% Free-living species per locality
30
20
10
0
BS QC BA EM LM
% Free-living specimens per locality
30
20
10
0
BS QC BA EM LM
% Massive species per locality
100
80
60
40
20
BS QC BA EM LM
% Massive specimens per locality
100
80
60
40
20
0
BS QC BA EM LM
% Platy species per locality
60
40
20
0
BS QC BA EM LM
% Platy specimens per locality
100
80
60
40
20
0
BS QC BA EM LM

Table 5.—Results of non-parametric tests comparing colony shape frequencies and % living species among the Limon reef trends.

| | | Kruskal-Wallis test | | | |
|---|---|---|---|---|---|
| Species subgroup | Data type | Corrected Chi-Square | df | p-value | Mann-Whitney U test results |
| branching | species | 16.987 | 4 | 0.002 | BA > EM > LM |
| | specimens | 19.360 | 4 | 0.001 | BA > EM > LM |
| free-living | species | 4.835 | 4 | 0.305 | BA = EM = LM |
| | specimens | 4.673 | 4 | 0.322 | BA = EM = LM |
| massive | species | 9.687 | 4 | 0.046 | EM > BA = LM |
| | specimens | 11.696 | 4 | 0.020 | EM > BA = LM |
| platy | species | 20.526 | 4 | 0.000 | LM > BA = EM |
| | specimens | 20.475 | 4 | 0.000 | LM > BA = EM |
| % living | species | 11.625 | 4 | 0.024 | BA = EM = LM; BA < LM |



Text-figure 8.—Maxima, medians, and minima of percentages of living species within each of five reef trends. The trends are arranged in chronological order from oldest (left) to youngest (right). BS, Brazo Seco patch; QC, Quebrada Chocolate trends; BA, Buenos Aires trend; EM, Empalme trend (including Santa Rosa patch); LM, Lomas del Mar trend.

or muddy environments at intermediate depths (10–30 m). The high percentages of branching corals in the Buenos Aires trend (and possibly the Quebrada Chocolate trends) suggest moderate exposure and shallow to intermediate water depths (<20 m). The high percentages of massive corals in the Empalme trend and associated Santa Rosa patch suggest exposed shallow conditions (<10 m) with high wave energies. The high percentage of free-living corals at the Brazo Seco patch suggests a shallow (<10 m) unstable substrate. Shallow-water indicators are common or abundant in localities within all five trends, and *Acropora palmata* is common or abundant at localities within the three younger trends. Nevertheless, deep-water indicators are common or abundant only in the Lomas del Mar trend, suggesting deep forereef environments. Thus, a mix of reef environments may be involved within each trend; and assignment of uniform depths to individual trends may be an over-simplification.

In summary, hermatypic corals indicate that reef environments changed from moderately exposed shallow and intermediate depth environments (Quebrada Chocolate and Buenos Aires trends), to exposed shallow environments (Empalme trend), to deep forereef environments (Lomas del Mar trend) within the Limon sequence through geologic time. Preliminary comparisons with microfossil and ahermatypic coral data collected in nearby sites generally support the interpretations based on hermatypic corals. Assemblages of benthic foraminifera suggest water depths of 50–100 m for the Lomas del Mar trend (Collins *et al.*, 1995) and 10–30 m for the Empalme trend (Collins in Jackson *et al.*, this volume). Ahermatypic corals suggest water depths of 40–73 m for the Lomas del Mar trend (Cairns, this volume). As mentioned above, more detailed comparisons between hermatypic corals and ostracodes are planned in future analyses.

## EVOLUTIONARY SIGNIFICANCE OF THE COLLECTED TAXA

Survey of the 73 Neogene to Recent Caribbean stratigraphic units in the 1996 Cenozoic Coral Database (CCD) compiled by Johnson and Budd (Budd and Johnson, 1997) indicates that unusually high numbers of global first and last occurrences of species occur within the Limon sequence (Table 4). A total of 39 first occurrences and 22 last occurrences takes place in the sequence. Among the first occurrences are those for 32 of the 60 species that currently live in the Caribbean. Several of these first occurrences are for important modern reef dominants, including *Acropora palmata* (see McNeill *et al.*, 1997), *A. cervicornis, Porites astreoides, P. furcata, Diploria strigosa, Montastraea faveolata,* and *M. franksi.* Last occurrences take place in many species that are abundant or common in the Mio-Pliocene of the Cibao Valley of the Dominican Republic (Budd *et al.*, 1996), including two species of *Stephanocoenia,* three species of *Porites,* and four species of *Montastraea.*

Closer examination of the first and last occurrence information (Table 4) shows that first occurrences take place in all five Limon reef trends, although the highest numbers of first occurrences are in the Buenos Aires trend and, to a lesser extent, the Lomas del Mar trend (Table 4). In fact, six of the seven modern reef dominants listed in the paragraph above first occur in the Buenos Aires trend. Two of these six (*Porites astreoides, Diploria strigosa*) also occur at approximately the same time in the Pinecrest Sandstone of Florida. In contrast, almost all of the observed last occurrences are concentrated in the Lomas del Mar trend.

Table 6.—Occurrences of species of *Stylophora*, *Acropora*, and *Caulastraea* within collections.

| PPP number | Locality code | Reef trend | *S. affinis* | *S. granulata* | *S. minor* | *S. monticulosa* | *A. cervicornis* | *A. palmata* | *C. portoricensis* |
|---|---|---|---|---|---|---|---|---|---|
| 1381 | BR | Brazo Seco | | | x | x | | | |
| 1386 | C2 | Q. Chocolate | | | | | x | | |
| 1384 | C4 | Q. Chocolate | x | | x | x | | | |
| 1316 | BA2 | Buenos Aires | | x | | x | x | | x |
| 1362 | BA2 | Buenos Aires | | | x | x | x | | |
| 1388 | BA2 | Buenos Aires | | | | | x | | x |
| 1346 | BA3 | Buenos Aires | | | | x | x | | x |
| 1125 | BA3 | Buenos Aires | | x | | | x | x | |
| 1345 | BA4 | Buenos Aires | | | | x | | | |
| 1364 | BA4 | Buenos Aires | | | | | | x | |
| 1348 | BA6 | Buenos Aires | | x | | | | | x |
| 1124 | BA6 | Buenos Aires | | | | | x | x | x |
| 1342 | BA7 | Buenos Aires | | x | | | x | x | x |
| 1343 | BA7 | Buenos Aires | | x | | x | x | x | x |
| 1344 | BA7 | Buenos Aires | | | | | x | x | x |
| 1366 | BA7 | Buenos Aires | | | | | x | x | x |
| 1341 | BA8 | Buenos Aires | | | | | x | x | x |
| 1428 | E1 | Empalme | | | | | | | x |
| 1340 | E2 | Empalme | | | | | | | x |
| 1374 | E3 | Empalme | | | | | | | x |
| 719 | SR1 | Santa Rosa | | | | | x | x | x |
| 1373 | SR2 | Santa Rosa | | | | | x | | x |
| 1499 | SR2 | Santa Rosa | | | | | | x | x |
| 1500 | SR2 | Santa Rosa | | | | | | x | x |
| 1351 | SR3 | Santa Rosa | | | | | x | | |
| 1372 | SR3 | Santa Rosa | | | | | | x | x |
| 1367 | SR4 | Santa Rosa | | | | | x | x | x |
| 1349 | LE1 | Lomas del Mar | | | | | | | x |
| 772 | LE1 | Lomas del Mar | | | | | x | | |
| 646 | LE2 | Lomas del Mar | | | | | x | | |
| 1106 | LE9 | Lomas del Mar | | | | | | x | |
| 1375 | LW1 | Lomas del Mar | | | | | | | x |
| 1331 | LW2 | Lomas del Mar | | | | | | x | |
| 1335 | P1 | Lomas del Mar | | | | | | x | |
| 1336 | P1 | Lomas del Mar | | | | | x | x | |
| 1337 | P1 | Lomas del Mar | | | | | | | x |
| 1338 | P1 | Lomas del Mar | | | | | x | x | x |
| 1339 | P1 | Lomas del Mar | | | | | | | x |
| 1353 | P2 | Lomas del Mar | | | | | | x | |
| 1126 | P2 | Lomas del Mar | | | | | | | x |
| 1127 | P2 | Lomas del Mar | | | | | x | x | |
| 1355 | P3 | Lomas del Mar | | | | | | x | |

Of the 82 species that occur in the Limon reef trends, 61 species (74.4%) originated within the past 11 million years (Table 4). Of these 61 species, 12 originated during the Late Miocene time (11.2–5.3 Ma), and five originated during Earliest Pliocene time (5.3–4 Ma). Twenty-seven of the remaining 41 species (65.8%) originated between 4–3 Ma, and 14 originated over the past two million years. Thus, approximately one-third of the fauna appears to have originated during a one-million year peak of origination at 4–3 Ma. In contrast, 29 of the 33 extinct species in the fauna (87.9%) became extinct during a one-million year peak of extinction at 2–1 Ma. These calculations (see Budd and Johnson, 1997, for further discussion of evolutionary rates) suggest that accelerated origination preceded accelerated extinction in these corals by 1–2 million years and, together with field observations, they indicate that members of the 'pre-turnover' (*i.e.*, Mio-Pliocene) and 'post-turnover' (*i.e.*, Recent) Caribbean reef coral faunas co-existed within the Limon sequence though the critical interval of faunal change on Caribbean reefs.

Percentages of living species collected within each trend range from <40% in the two older reef trends to >70% in the two younger trends, and thus further support the transitional interpretation for the fauna. Per-

Table 7.—Occurrence matrix of species of 27 Costa Rica and 3 Panama localities. Species are in taxonomic order; localities are arranged by reef trend. Occurrences are coded relative to abundance: 'R' = rare, 'C' = common, 'A' = abundant, 'F' = super-abundant.

| Genus | Species | CCD species ID number | BS | C4 | BA1 | BA2 | BA3 | BA4 | BA6 | BA7 | BA8 | E3 | SR1 | SR2 | SR3 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Stephanocoenia* | *intersepta* | 2 | | | | | | | | | | | | R | |
| *Stephanocoenia* | *duncani* | 3 | | A | | R | C | | | R | | | C | C | C |
| *Stephanocoenia* | *spongiformis* | 4 | | | | | | | | | | | | | |
| *Stylophora* | *affinis* | 5 | | C | | | | | | | | | | | |
| *Stylophora* | *granulata* | 7 | | | | C | C | | C | C | | | | | |
| *Stylophora* | *minor* | 9 | C | C | | R | | | | | | | | | |
| *Stylophora* | *monticulosa* | 10 | R | C | | C | C | C | | R | | | | | |
| *Pocillopora* | *crassoramosa* | 15 | F | | | | | | | | | | | | |
| *Madracis* | *asperula* | 16.5 | | | | | | | | | | | | | |
| *Madracis* | *decactis* | 17 | R | | | | | | | | | | | | |
| *Madracis* | *mirabilis* | 20 | | | | | | | | | | | R | R | |
| *Madracis* | *pharensis* | 21 | | | | | | | | | | | | | |
| *Madracis* | sp. A | 21.5 | C | | | | | | | | | | | | |
| *Acropora* | *cervicornis* | 22 | | C | | F | A | | C | A | A | | C | C | |
| *Acropora* | *palmata* | 23 | | | | | A | | A | C | A | | C | C | C |
| *Agaricia* | *grahamae* | 29 | | | | | | | | | | | | | |
| *Agaricia* | *lamarcki* | 30 | | | | | | | | | | | | | |
| *Agaricia* | *undata* | 32 | | | | | | | | | | | | | |
| *Undaria* | *agaricites* | 33 | | A | C | A | C | | A | C | C | | R | A | A |
| *Undaria* | *crassa* | 34 | C | C | | | | | | C | C | | | | C |
| *Undaria* | *pusilla* | 35 | R | | | | | | | | | | | | R |
| *Helioseris* | *cucullata* | 43 | C | R | | C | C | | R | C | | | | | |
| *Siderastrea* | *radians* | 56 | | | | | C | | | | | | | | |
| *Siderastrea* | *siderea* | 58 | | | | | C | | | C | C | | C | A | C |
| *Porites* | *astreoides* | 63 | | | | R | | C | R | A | | C | R | C | C |
| *Porites* | *portoricensis* | 65 | | R | C | | | C | | | | C | | | |
| *Porites* | *waylandi* | 68 | | | | | | | | | | | | | |
| *Porites* | *baracoaensis* | 69 | R | | C | | | C | R | C | | | | | |
| *Porites* | *branneri* | 70 | | | | | | | | | | | | | |
| *Porites* | *colonensis* | 73 | | | | | | | | | | | | | |
| *Porites* | *furcata* | 76 | | | F | C | C | C | A | C | | | R | A | |
| *Porites* | *porites* | 77 | | | | | C | | | | | | | C | |
| *Caulastraea* | *portoricensis* | 83 | | | | C | C | | A | A | C | | | A | C |
| *Favia* | *fragum* | 88 | | R | C | | | C | | C | C | | | | |
| *Diploria* | *clivosa* | 94 | R | | | | C | | | R | C | | | C | R |
| *Diploria* | *labyrinthiformis* | 95 | | | | R | | | | C | | A | | | |
| *Diploria* | *strigosa* | 97 | | | C | | C | C | R | C | A | C | | R | C |
| *Manicina* | *areolata* | 100 | | | | | | | C | C | | | R | C | C |
| *Manicina* | *mayori* | 101 | | | | | | | | C | | | | | |
| *Manicina* | *puntagordensis* | 102 | | | | | | | | C | | | | | |
| *Thysanus* | sp. A | 109 | | C | | R | | | C | C | | | | C | |
| *Thysanus* | *corbicula* | 111 | | | | | | | | | | | | | |
| *Colpophyllia* | *amaranthus* | 112 | | | | R | | | | | | | C | | |
| *Colpophyllia* | *natans* | 114 | | | C | C | C | | | | | A | R | | R |
| *Colpophyllia* | sp. A | 114.5 | | | | | | | | R | | | | C | |
| *Montastraea* | *faveolata* | 117 | | | | | | C | | C | | | | | C |
| *Montastraea* | *franksi* | 118 | | | | A | | C | C | | | | | R | |
| *Montastraea* | *limbata*-1 | 121.1 | | | | | | | C | C | | | | | R |
| *Montastraea* | *limbata*-2 | 121.2 | | C | | | | | C | A | C | | C | C | C |
| *Montastraea* | sp. A | 122 | C | | | C | | | C | C | | | R | | C |
| *Montastraea* | *canalis* | 124 | | | | | | | | | | | | | R |
| *Montastraea* | *cavernosa*-2 | 126 | | C | | C | | | | R | | C | | | C |
| *Montastraea* | *cavernosa*-3 | 127 | | | | | | | | | | C | R | | |
| *Montastraea* | *cylindrica* | 128 | | | | | | | | | | C | | | |
| *Solenastrea* | *bournoni* | 131 | C | A | | | | | | | | | | | A |

Table 7.—Continued.

| SR4 | LE1 | LE2 | LE3 | LE4 | LE5 | LE7 | LE8 | LE9 | LE10 | LW2 | LW3 | P1 | P2 | HP | PA | FH | No. of Costa Rica localities | No. of Panama localities |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | C | C | C | C | C | C | C | A | C | | R | | | | | 11 | 0 |
| C | C | A | | C | A | A | A | A | A | C | C | C | | | | C | 19 | 1 |
| | | | | C | R | | | R | | | | | | | | | 3 | 0 |
| | | | | | | | | | | | | | | C | | | 1 | 1 |
| | | | | | | | | | | | | | | A | | | 4 | 1 |
| | | | | | | | | | | | | | | | | | 3 | 0 |
| | | | | | | | | | | | | | | | | C | 6 | 1 |
| | | | | | | | | | | | | | | | | C | 2 | 1 |
| | | R | | C | C | | | C | A | | | | | | | | 5 | 0 |
| | | C | | A | A | C | | C | A | C | C | | R | C | | | 11 | 1 |
| | A | A | C | A | C | C | C | C | C | | | | | | | | 11 | 0 |
| | | | | | | | | R | | | | | | | | | 1 | 0 |
| | | | | | | | | | | | | | | | | | 1 | 0 |
| C | C | R | | | | | | | | | | C | R | C | | | 14 | 1 |
| A | | | | | | | | R | | R | | C | C | C | | | 12 | 1 |
| | C | F | A | A | A | C | C | A | A | C | C | | | | | | 11 | 0 |
| | C | A | A | A | C | R | C | A | A | C | C | C | | | | | 12 | 0 |
| | C | A | C | C | C | | R | A | A | A | C | | | | | | 10 | 0 |
| | F | F | F | A | A | A | A | A | A | A | A | A | F | A | C | C | 23 | 3 |
| C | C | | | R | | | | R | | | | A | | C | | | 10 | 1 |
| | | | | | | | | | | | | R | R | | | | 4 | 0 |
| | C | R | C | R | | R | | | R | | | C | R | C | C | | 14 | 2 |
| | C | | | | | | | | | | | | | | | | 2 | 0 |
| | C | R | C | | C | C | | R | C | R | | C | | | C | | 15 | 1 |
| C | C | R | | | | | | C | C | | | A | R | C | C | | 15 | 2 |
| | | | | C | | | | | | | | | | | | | 5 | 0 |
| | | | | | | | R | | | | | | | | | | 1 | 0 |
| | | | | | | | C | | | | | | | | | | 6 | 0 |
| | | C | | C | C | | | | R | R | | | | | | | 5 | 0 |
| | | C | | C | | C | | | C | | | | | | | | 4 | 0 |
| | A | | | | | | | | | C | | | | | | | 10 | 0 |
| | | | | | | | | | | | | | | | | | 2 | 0 |
| C | C | | | | | | | | | | | C | R | A | | | 11 | 1 |
| | | | | | | | | | | | | | | | | | 5 | 0 |
| C | | | | | | | | | | | | | | | | | 7 | 0 |
| | | | | | | C | | | | | | C | | | C | | 5 | 1 |
| A | | | | | C | R | | | R | R | | A | A | | A | C | 16 | 2 |
| | | R | | C | | R | | R | C | | | | | C | | | 10 | 1 |
| C | C | | | | | R | | | C | | | C | C | | | | 7 | 0 |
| | | R | | C | R | | | C | C | | | | | | | C | 6 | 1 |
| | | | | | | | | | | | | | | | | | 5 | 0 |
| | | | | | | | | | | | | | | | | C | 0 | 1 |
| | | | | | | | | | | | | | | | | | 2 | 0 |
| | C | R | | | | R | C | C | C | R | | C | | | A | | 14 | 1 |
| | | | | | | | | | R | | | C | R | A | C | | 5 | 2 |
| | C | | | | C | C | R | C | C | | | A | A | C | A | | 11 | 2 |
| | | | | R | C | | | R | C | C | | C | | | C | | 10 | 1 |
| | | | | | | R | | | | | | | | | | | 4 | 0 |
| | | C | | | C | C | C | | A | R | | | C | | | | 14 | 0 |
| C | | | | | | | | | | | | R | | | | | 8 | 0 |
| C | | C | | C | | | | R | C | | | R | | | | | 7 | 0 |
| | C | | C | | C | A | | R | | | C | C | C | | | | 13 | 0 |
| | | | | C | R | | R | R | | | | | | | | | 6 | 0 |
| | | C | C | C | A | A | A | A | A | C | C | | R | | | | 12 | 0 |
| | C | | | | | | | | | | | C | | | | | 5 | 0 |

Table 7.—Continued.

| Genus | Species | CCD species ID number | BS | C4 | BA1 | BA2 | BA3 | BA4 | BA6 | BA7 | BA8 | E3 | SR1 | SR2 | SR3 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Antillophyllia* | *sawkinsi* | 137 | | | | | | | | | | | | | |
| *Meandrina* | *braziliensis* | 138 | | | | | | | | | | | | | |
| *Meandrina* | *meandrites* | 139 | | | | | | | | | | C | | | |
| *Meandrina* | sp. A | 139.5 | | | | | | | | | | | | | |
| *Placocyathus* | *trinitatis* | 143 | C | | | | | | | | | | | | |
| *Placocyathus* | *variabilis* | 144 | A | R | | | | | | | | | | | |
| *Dichocoenia* | *caloosahatcheensis* | 145 | | | | | | | | | | | | R | |
| *Dichocoenia* | *eminens* | 146 | | C | | | | | | | | | | | |
| *Dichocoenia* | *stokesi* | 148 | | | | | | C | C | C | | | C | C | |
| *Dichocoenia* | *stellaris* | 149 | | | | | | | | | | | R | | |
| *Dichocoenia* | *tuberosa* | 150 | R | R | | | | | | R | | | | | |
| *Archohelia* | *limonensis* | 152.5 | | | | | | | | | | | | | |
| *Scolymia* | *cubensis* | 155 | | | | | | | | | | | | | |
| *Scolymia* | *lacera* | 157 | | | | | | | | | | | | | |
| *Mussa* | *angulosa* | 158 | | | | R | | | | | | | | | R |
| *Mussismilia* | aff. *M. hartti* | 160.5 | | | | | | | C | | | | R | | |
| *Isophyllastrea* | sp. B | 164.5 | | | | | | | | R | | | | | |
| *Mycetophyllia* | *aliciae* | 166 | | | | | | | | | | | | | |
| *Mycetophyllia* | *danaana* | 168 | | | | | | | | | | | | | |
| *Mycetophyllia* | *ferox* | 169 | | | | | | | | | | | | | R |
| *Mycetophyllia* | *lamarckiana* | 170 | | | | | | | | | | | | | |
| *Mycetophyllia* | *reesi* | 171 | | | | | | | | | | | | | |
| *Mycetophyllia* | sp. A | 171.5 | | | | | | | | | | | | | |
| *Eusmilia* | *fastigiata* | 173 | | | | | | | | | | | R | | |
| *Eusmilia* | sp. A | 175 | | C | | | | | | | | | | | |
| | Number of species | 80 | 15 | 18 | 7 | 18 | 15 | 10 | 18 | 30 | 10 | 9 | 18 | 21 | 21 |

centages of living species collected within each locality are statistically lower in the Brazo Seco and Quebrada Chocolate trends than in the Buenos Aires, Empalme, and Lomas del Mar trends (Table 5, Text-fig. 8).

Also supporting the transitional interpretation are the co-occurrences of species of *Stylophora, Acropora,* and *Caulastraea* at individual collection sites, and within localities (Table 6). *Stylophora* and *Caulastraea,* two genera that are now extinct in the Caribbean, dominated shallow and intermediate depth reef environments in *pre-turnover* faunas; whereas *Acropora* has dominated these same environments in *post-turnover* faunas (Budd and Kievman, in press). Much of the shift between these two distinctly different sets of community dominants takes place in the Late Pliocene and Early Pleistocene, between 4–1 Ma. However, *Acropora palmata,* the species that sometimes dominates modern Caribbean reef crests, does not become extremely abundant in reef coral assemblages until the Late Pleistocene (Jackson, 1994; Jackson and Budd, 1996).

Four species of *Stylophora,* two species of *Acropora,* and one species of *Caulastraea* occur at a total of 42 of the 107 collection sites and 24 of the 34 localities (Table 6). Species of *Stylophora* occur at 10 collection sites (7 localities) in the three older reef trends; species of *Acropora* occur at 30 collection sites (18 localities) in the four younger trends; and the one species of *Caulastraea* occurs at 25 collection sites (16 localities) in the three younger trends. Species of *Stylophora* and *Acropora* co-occur at seven sites (PPP 1125, 1316, 1342, 1343, 1346, 1362, 1388) and five localities (BA2, BA3, BA4, BA6, BA7) in the Buenos Aires trend; *Acropora palmata* itself co-occurs with species of *Stylophora* at three Buenos Aires sites (PPP 1125, 1342, 1343). Species of *Caulastraea* and *Acropora* co-occur at 16 sites and 12 localities within the three younger trends. These co-occurrences support the notion that dominant members of pre- and post-turnover faunas lived side by side in the same environment.

## ASSEMBLAGE ANALYSES

### OCCURRENCE MATRIX

We used the specimen database to assemble an occurrence matrix (78 species × 27 localities) containing codes for relative abundances (Table 7). Counts of specimens were obtained for species within each lo-

Table 7.—Continued.

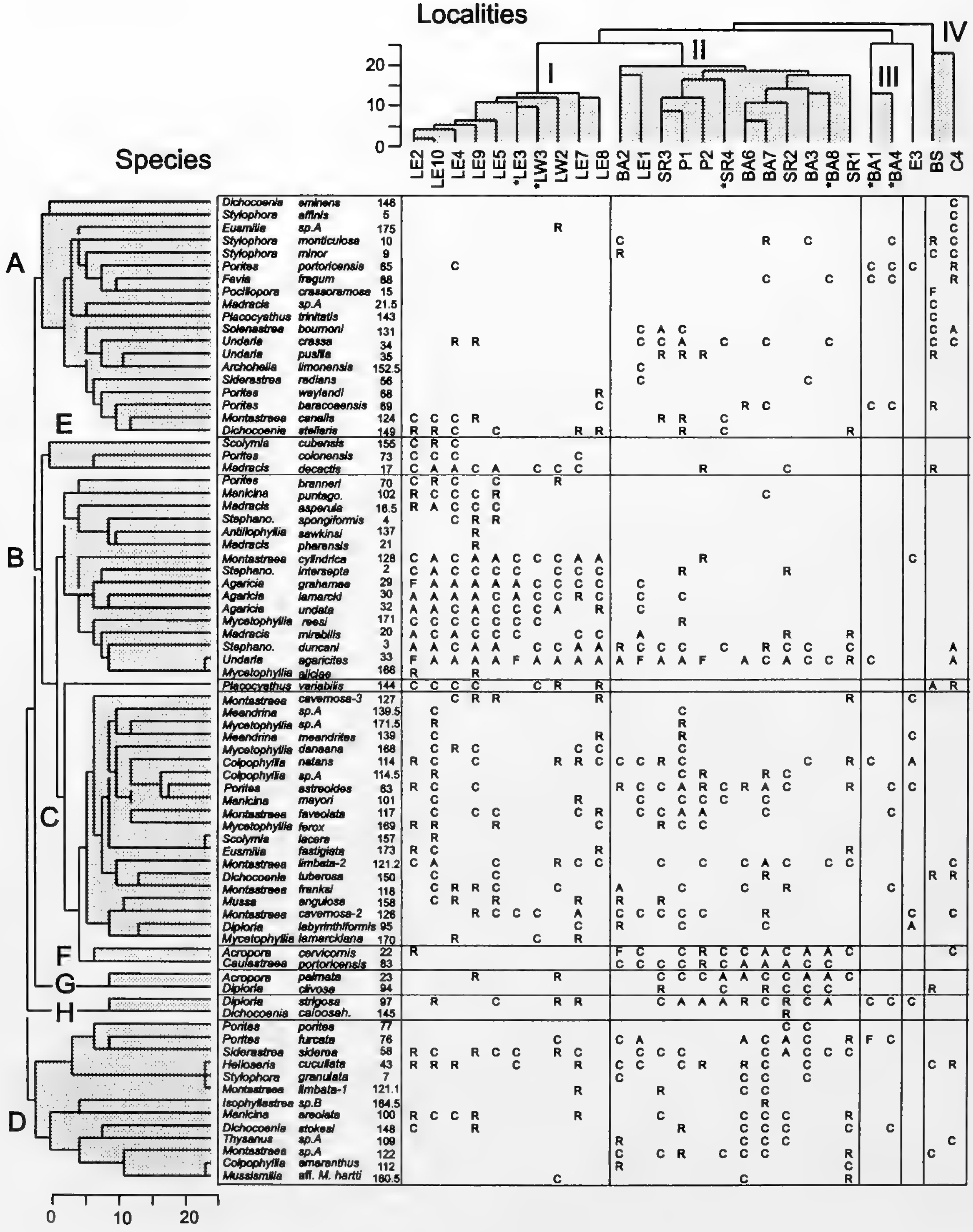
| SR4 | LE1 | LE2 | LE3 | LE4 | LE5 | LE7 | LE8 | LE9 | LE10 | LW2 | LW3 | P1 | P2 | HP | PA | FH | No. of Costa Rica localities | No. of Panama localities |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | R | | | | | | | | | 1 | 0 |
| | | | | | | | | | | | | | | | | A | 0 | 1 |
| | | | | | | | R | | C | | | R | | | C | | 4 | 1 |
| | | | | | | | | | C | | | C | | C | A | | 2 | 2 |
| | | | | | | | | | | | | | | | | | 1 | 0 |
| | | C | | C | | | R | C | C | R | C | | | | | F | 9 | 1 |
| | | | | | | | | | | | | | | | | | 1 | 0 |
| | | | | | | | | | | | | | | | | C | 1 | 1 |
| | | C | | | | | | R | | | | R | | | | | 8 | 0 |
| C | | R | | C | C | R | R | | R | | | R | | | | | 9 | 0 |
| | | | | | C | | | | C | | | | | | | | 5 | 0 |
| | C | | | | | | | | | | | | | | | | 1 | 0 |
| | | C | | C | | | | | R | | | | | | | | 3 | 0 |
| | | | | | | | | | R | | | | | | | | 1 | 0 |
| | | | | R | R | R | | | C | | | | | | | | 6 | 0 |
| | | | | | | | | | | C | | | | | | | 3 | 0 |
| | | | | | | | | | | | | | | | | | 1 | 0 |
| | | R | | | | | | R | | | | | | | | | 2 | 0 |
| | | | | R | | C | C | C | C | | | C | | C | | | 6 | 1 |
| | | R | | | R | | C | | R | | | C | C | | C | | 7 | 1 |
| | | | | R | | R | | | | | C | | | | | | 3 | 0 |
| | | C | C | C | C | | | C | C | | C | R | | | | | 8 | 0 |
| | | | | | | | | | R | | | R | | | | | 2 | 0 |
| | | R | | | | | R | | C | | | | | | | | 4 | 0 |
| | | | | | | | | | | R | | | | | | | 2 | 0 |
| 12 | 20 | 29 | 11 | 28 | 25 | 24 | 20 | 30 | 38 | 19 | 11 | 31 | 16 | 15 | 13 | 10 | 524 | 38 |

cality, and codes for rare, common, abundant, and super-abundant were assigned using a modified version of the 'proportion of species' method described by Gaston (1994). In this procedure, beginning with the lowest specimen counts for a given locality, approximately 25% or less of the species were designated as rare, 50% or more were designated as common, and 25% or less were designated as abundant. Only in cases where the highest count exceeded the next highest count by two times were species designated as super-abundant. In counting specimens, specimens with identification confidence codes of <25% were counted as only one-half. If the total specimen count for a species within a locality was only one-half, the species was deleted from the data set.

### CLASSIFICATION (CLUSTER ANALYSIS)

To determine if the assemblages could be separated into discrete groups, we first analyzed the occurrence matrix using average linkage cluster analysis (SPSS for Windows, version 6.1, 1994). We performed analyses for both localities (Q-mode) and species (R-mode), and used both relative abundance (frequency count) codes and presence-absence (binary) data. When analyses were performed with relative abundance codes, the Phi-square coefficient was used. As explained by Shi (1993) and Hayek (1994), the Phi coefficient is a traditional measure of association, similar to a chi-square statistic but normalized relative to frequency so that it is less affected by sample size. When analyses were performed with binary data, the Lance and Williams coefficient was used. The Lance and Williams coefficient is similar to a Dice or Bray-Curtis similarity coefficient; both give more weight to joint presences and exclude joint absences.

The results using relative abundance codes (Text-fig. 9) suggest four clusters of localities [two large clusters (I and II) and two small clusters (III and IV)] and eight clusters of species [(four large clusters (A to D) and four small clusters (E to H)]. Locality cluster I consists of 10 localities within the Lomas del Mar trend; locality cluster II consists of 12 localities within the Buenos Aires trend, the Lomas del Mar trend, and the Santa Rosa patch of the Empalme trend; locality cluster III consists of two localities within the Buenos Aires trend that have low sample sizes; and locality cluster IV consists of the two localities in the two stratigraphically older trends. The one locality within the



| | | | LE2 | LE10 | LE4 | LE9 | LE5 | *LE3 | *LW3 | LW2 | LE7 | LE8 | BA2 | LE1 | SR3 | P1 | P2 | *SR4 | BA6 | BA7 | SR2 | BA3 | *BA8 | SR1 | *BA1 | *BA4 | E3 | BS | C4 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Dichocoenia* | *eminens* | 146 | | | | | | | | | | | | | | | | | | | | | | | | | | | C |
| *Stylophora* | *affinis* | 5 | | | | | | | | | | | | | | | | | | | | | | | | | | | C |
| *Eusmilia* | *sp.A* | 175 | | | | | | | | R | | | | | | | | | | | | | | | | | | | C |
| *Stylophora* | *monticulosa* | 10 | | | | | | | | | | | C | | | | | | | R | | C | | | | C | | R | C |
| *Stylophora* | *minor* | 9 | | | | | | | | | | | R | | | | | | | | | | | | | | | C | C |
| *Porites* | *portoricensis* | 65 | | | C | | | | | | | | | | | | | | | | | | | | C | C | C | | R |
| *Favia* | *fragum* | 88 | | | | | | | | | | | | | | | | | | C | | | C | | C | C | | | R |
| *Pocillopora* | *crassoramosa* | 15 | | | | | | | | | | | | | | | | | | | | | | | | | | F | |
| *Madracis* | *sp.A* | 21.5 | | | | | | | | | | | | | | | | | | | | | | | | | | C | |
| *Placocyathus* | *trinitatis* | 143 | | | | | | | | | | | | | | | | | | | | | | | | | | C | |
| *Solenastrea* | *bournoni* | 131 | | | | | | | | | | | | C | A | C | | | | | | | | | | | | C | A |
| *Undaria* | *crassa* | 34 | | | R | R | | | | | | | | C | C | A | | C | | C | | | C | | | | | C | C |
| *Undaria* | *pusilla* | 35 | | | | | | | | | | | | | R | R | R | | | | | | | | | | | R | |
| *Archohelia* | *limonensis* | 152.5 | | | | | | | | | | | | C | | | | | | | | | | | | | | | |
| *Siderastrea* | *radians* | 56 | | | | | | | | | | | | C | | | | | | | | C | | | | | | | |
| *Porites* | *waylandi* | 68 | | | | | | | | | | R | | | | | | | | | | | | | | | | | |
| *Porites* | *baracoaensis* | 69 | | | | | | | | | | C | | | | | | | R | C | | | | | C | C | | R | |
| *Montastraea* | *canalis* | 124 | C | C | C | R | | | | | | | | | R | R | | C | | | | | | | | | | | |
| *Dichocoenia* | *stellaris* | 149 | R | R | C | | C | | | | R | R | | | | R | | C | | | | | | R | | | | | |
| *Scolymia* | *cubensis* | 155 | C | R | C | | | | | | | | | | | | | | | | | | | | | | | | |
| *Porites* | *colonensis* | 73 | C | C | C | | | | | | C | | | | | | | | | | | | | | | | | | |
| *Madracis* | *decactis* | 17 | C | A | A | C | A | | C | C | C | | | | | | R | | | | C | | | | | | | R | |
| *Porites* | *branneri* | 70 | C | R | C | | C | | | R | | | | | | | | | | | | | | | | | | | |
| *Manicina* | *puntago.* | 102 | R | C | C | C | R | | | | | | | | | | | | | C | | | | | | | | | |
| *Madracis* | *asperula* | 16.5 | R | A | C | C | C | | | | | | | | | | | | | | | | | | | | | | |
| *Stephano.* | *spongiformis* | 4 | | | C | R | R | | | | | | | | | | | | | | | | | | | | | | |
| *Antillophyllia* | *sawkinsi* | 137 | | | | R | | | | | | | | | | | | | | | | | | | | | | | |
| *Madracis* | *pharensis* | 21 | | | | R | | | | | | | | | | | | | | | | | | | | | | | |
| *Montastraea* | *cylindrica* | 128 | C | A | C | A | A | C | C | C | A | A | | | | | R | | | | | | | | | | C | | |
| *Stephano.* | *intersepta* | 2 | C | A | C | C | C | C | | C | C | C | | | | R | | | | | R | | | | | | | | |
| *Agaricia* | *grahamae* | 29 | F | A | A | A | A | A | C | C | C | C | | C | | | | | | | | | | | | | | | |
| *Agaricia* | *lamarcki* | 30 | A | A | A | A | C | A | C | C | R | C | | C | | C | | | | | | | | | | | | | |
| *Agaricia* | *undata* | 32 | A | A | C | A | C | C | C | A | | R | | C | | | | | | | | | | | | | | | |
| *Mycetophyllia* | *reesi* | 171 | C | C | C | C | C | C | C | | | | | | | R | | | | | | | | | | | | | |
| *Madracis* | *mirabilis* | 20 | A | C | A | C | C | C | | | C | C | | A | | | | | | | R | | | R | | | | | |
| *Stephano.* | *duncani* | 3 | A | A | C | A | A | | C | C | A | A | R | C | C | C | | C | | R | C | C | | C | | | | | A |
| *Undaria* | *agaricites* | 33 | F | A | A | A | A | F | A | A | A | A | A | F | A | A | F | | A | C | A | C | C | R | C | | | | A |
| *Mycetophyllia* | *aliciae* | 166 | R | | | R | | | | | | | | | | | | | | | | | | | | | | | |
| *Placocyathus* | *variabilis* | 144 | C | C | C | C | | | C | R | | R | | | | | | | | | | | | | | | | A | R |
| *Montastraea* | *cavernosa-3* | 127 | | | C | R | R | | | | | R | | | | | | | | | | | | R | | | C | | |
| *Meandrina* | *sp.A* | 139.5 | | C | | | | | | | | | | | | C | | | | | | | | | | | | | |
| *Mycetophyllia* | *sp.A* | 171.5 | | R | | | | | | | | | | | | R | | | | | | | | | | | | | |
| *Meandrina* | *meandrites* | 139 | | C | | | | | | | | R | | | | R | | | | | | | | | | | C | | |
| *Mycetophyllia* | *danaana* | 168 | | C | R | C | | | | | C | C | | | | C | | | | | | | | | | | | | |
| *Colpophyllia* | *natans* | 114 | R | C | | C | | | | R | R | C | C | C | R | C | | | | | | C | | R | C | | A | | |
| *Colpophyllia* | *sp.A* | 114.5 | | R | | | | | | | | | | | | C | R | | | R | C | | | | | | | | |
| *Porites* | *astreoides* | 63 | R | C | | C | | | | | | | R | C | C | A | R | C | R | A | C | | | R | | C | C | | |
| *Manicina* | *mayori* | 101 | | C | | | | | | | R | | | C | | C | C | C | | C | | | | | | | | | |
| *Montastraea* | *faveolata* | 117 | | C | | C | C | | | | C | R | | C | C | A | A | | | C | | | | | | C | | | |
| *Mycetophyllia* | *ferox* | 169 | R | R | | | R | | | | | C | | | R | C | C | | | | | | | | | | | | |
| *Scolymia* | *lacera* | 157 | | R | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Eusmilia* | *fastigiata* | 173 | R | C | | | | | | | | R | | | | | | | | | | | | R | | | | | |
| *Montastraea* | *limbata-2* | 121.2 | C | A | | | C | | | R | C | C | | | C | | C | | C | A | C | | C | C | | | | | C |
| *Dichocoenia* | *tuberosa* | 150 | | C | | | C | | | | | | | | | | | | | R | | | | | | | | R | R |
| *Montastraea* | *franksi* | 118 | | C | R | R | C | | | C | | | A | | | C | | | C | | R | | | | | C | | | |
| *Mussa* | *angulosa* | 158 | | C | R | | R | | | | R | | R | | R | | | | | | | | | | | | | | |
| *Montastraea* | *cavernosa-2* | 126 | | | | R | C | C | C | | A | | C | C | C | C | C | | | R | | | | | | | C | | C |
| *Diploria* | *labyrinthiformis* | 95 | | | | | | | | | C | | R | | | C | | | | C | | | | | | | A | | |
| *Mycetophyllia* | *lamarckiana* | 170 | | | R | | | | C | | R | | | | | | | | | | | | | | | | | | |
| *Acropora* | *cervicornis* | 22 | R | | | | | | | | | | F | C | | C | R | C | C | A | C | A | A | C | | | | | C |
| *Caulastraea* | *portoricensis* | 83 | | | | | | | | | | | C | C | C | C | R | C | A | A | A | C | C | | | | | | |
| *Acropora* | *palmata* | 23 | | | | R | | | | R | | | | | C | C | C | A | A | C | C | A | A | C | | | | | |
| *Diploria* | *clivosa* | 94 | | | | | | | | | | | | | R | | | C | | R | C | C | C | | | | | R | |
| *Diploria* | *strigosa* | 97 | | R | | | C | | | R | R | | | | C | A | A | A | R | C | R | C | A | | C | C | C | | |
| *Dichocoenia* | *caloosah.* | 145 | | | | | | | | | | | | | | | | | | | R | | | | | | | | |
| *Porites* | *porites* | 77 | | | | | | | | | | | | | | | | | | | C | C | | | | | | | |
| *Porites* | *furcata* | 76 | | | | | | | | C | | | C | A | | | | | A | C | A | C | | R | F | C | | | |
| *Siderastrea* | *siderea* | 58 | R | C | | R | C | C | | R | C | | | C | C | C | | | | C | A | C | C | C | | | | | |
| *Helioseris* | *cucullata* | 43 | R | R | R | | | C | | | R | | C | C | | C | R | | R | C | | C | | | | | | C | R |
| *Stylophora* | *granulata* | 7 | | | | | | | | | | | C | | | | | | C | C | | C | | | | | | | |
| *Montastraea* | *limbata-1* | 121.1 | | | | | | | | | R | | | | R | | | | C | C | | | | | | | | | |
| *Isophyllastrea* | *sp.B* | 164.5 | | | | | | | | | | | | | | | | | | R | | | | | | | | | |
| *Manicina* | *areolata* | 100 | R | C | C | R | | | | | R | | | | C | | | | C | C | C | | | R | | | | | |
| *Dichocoenia* | *stokesi* | 148 | C | | | R | | | | | | | | | | R | | | C | C | C | | | C | | C | | | |
| *Thysanus* | *sp.A* | 109 | | | | | | | | | | | R | | | | | | C | C | C | | | | | | | | C |
| *Montastraea* | *sp.A* | 122 | | | | | | | | | | | C | | C | R | | C | C | C | | | | R | | | | C | |
| *Colpophyllia* | *amaranthus* | 112 | | | | | | | | | | | R | | | | | | | | | | | C | | | | | |
| *Mussismilia* | *aff. M. hartti* | 160.5 | | | | | | | | C | | | | | | | | | C | | | | | R | | | | | |

Empalme trend proper does not belong to any of the four clusters. Removal of locality cluster I (the Lomas del Mar trend) from the analysis results in exactly the same pattern of relationships among localities within locality cluster II; thus, the unexpected grouping of localities from three stratigraphically separate reef trends in locality cluster II appears to be robust.

The results using relative abundance codes (Text-fig. 9) further indicate that the similarities among species are low; therefore, clusters can only be defined at very high levels. Several species are abundant or common in more than one locality cluster, implying considerable overlap in species composition among locality clusters. Locality cluster I is characterized by species clusters B and E, which contain low numbers of extinct species (5 out of 19) that are predominantly platy and massive. Locality cluster II is characterized by species clusters D, F, G, and H, which contain slightly higher numbers of extinct species (7 out of 19) that are predominantly branching and massive. Locality cluster IV is characterized by species cluster A, which contains a high proportion of extinct species (13 out of 19). The single Empalme branch appears to be characterized by species cluster C; however, species within cluster C are common throughout all four locality clusters. Locality cluster III is composed of two localities with low sample sizes and does not seem to correspond with any species clusters.

Q-mode results using binary data reveal exactly the same locality clusters as those found using relative abundance codes; however, R-mode results using binary data show important differences among species clusters. Most notably, species previously belonging to species cluster C no longer group together and are scattered across the dendrogram.

In general, the large amount of overlap in species composition among locality clusters and the instability of the R-mode results indicate that distinct clusters and associations among species do not exist within these data, and that the assemblages are not discrete. Distinct clusters would be expected if species within communities responded similarly either to short-term changes in the local environment *or* to long-term evolutionary changes. When localities in the deep forereef trend (Lomas del Mar) are removed and only shallow and intermediate environments are included in the analysis, the clusters continue to overlap, indicating that evolutionary changes in the fauna during this interval were not simultaneous. These results agree with the origination and extinction data of the previous section (Table 4) and the increasing percentages of living species from older to younger reef trends (Text-fig. 8), and they provide additional support for the interpretation that the fauna was transitional during the two million year interval between 3.6–1.6 Ma.

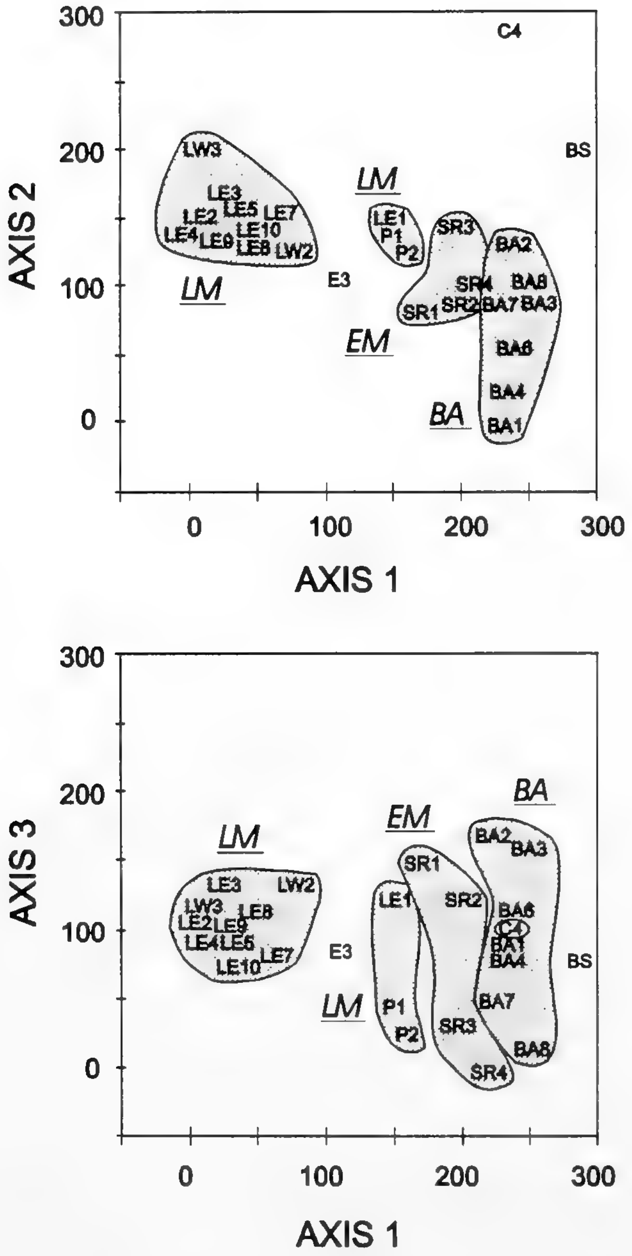
### ORDINATION (DETRENDED CORRESPONDENCE ANALYSES)

In order to determine the major directions of variation among the assemblages in the sequence and to search further for environmental and evolutionary gradients of faunal change in the data, we analyzed the occurrence matrix using a linear ordination technique known as 'detrended correspondence analysis' (PC-ORD, version 2.0, McCune and Mefford, 1995). The purpose of ordination is to produce a representation of the data in low-dimensional space, in which similar species and samples are close together and dissimilar entities are far apart. The resulting axes are interpreted using independent environmental and evolutionary data. We selected a linear ordination technique, detrended correspondence analysis (DCA), over another commonly used nonlinear ordination technique, nonmetric multidimensional scaling (NMDS), because DCA is more effective at revealing linear gradients in the data (Gauch, 1982). DCA has the added advantage of using chi-square distances (metric values) and not rank-order dissimilarities (as in NMDS). Unlike DCA, NMDS preserves relative and not absolute dissimilarities. Furthermore, DCA simultaneously ordinates localities and species in 3-dimensional space, thus alleviating problems associated with choice in numbers of axes and axis interpretation (Shi, 1993).

DCA is a form of reciprocal averaging in which species ordination scores are averages of sample ordination scores and, reciprocally, sample ordination scores are averages of species ordination scores. The procedure is iterative and begins with arbitrary species ordination scores, which in turn are used to calculate sample ordination scores. The sample ordination scores are then used to obtain species ordination scores. Iterations are continued until the scores stabilize. Detrending is applied to sample scores at each iteration to rescale the axes and correct for arch effects (Gauch, 1982).

←

Text-figure 9.—Q-mode (localities) and R-mode (species) cluster analysis of relative abundance code data. Clusters of localities (labeled 'I' through 'IV') and clusters of species (labeled 'A' through 'H') are defined on the basis of their descriptive utility and not on the basis of cutoff levels. Abbreviations for localities are given in Table 1. Occurrences are coded as 'R' for rare, 'C' for common, 'A' for abundant, and 'F' for super-abundant.



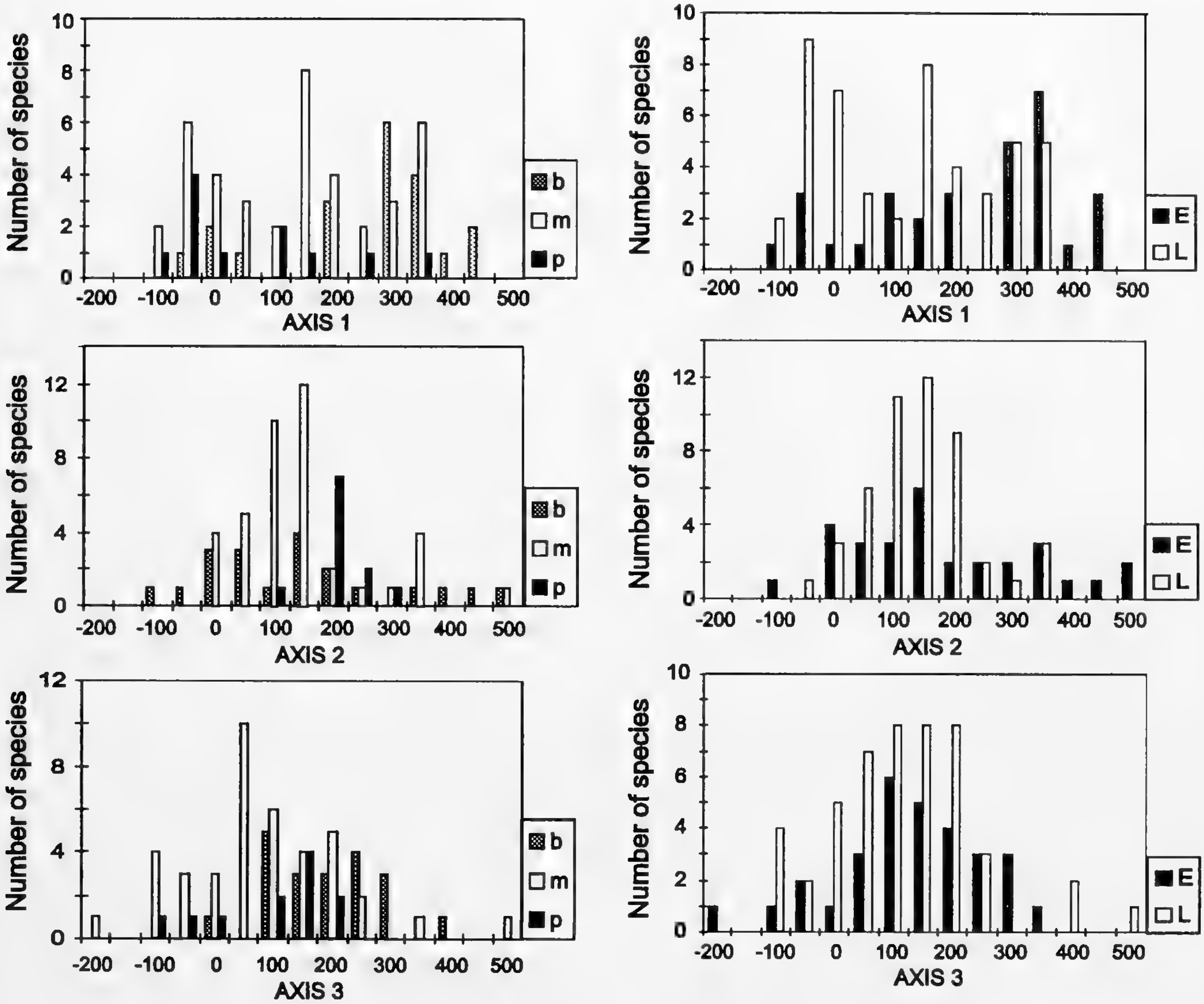
Text-figure 10.—Scatterplots of DCA scores for 27 Costa Rican localities determined using relative abundance code data. Each point represents a locality, the abbreviations for which are given in Table 1. Shaded areas encompass localities within the Buenos Aires (BA), Empalme (EM), and Lomas del Mar (LM) reef trends. The Lomas del Mar localities are divided into two subsets based on cluster analysis results: (1) 10 tightly clustered localities (LE2, LE3, LE4, LE5, LE7, LE8, LE9, LE10, LW2, LW3) that are scattered across the top of the topographic ridge formed by the Lomas del Mar trend, and (2) three localities (LE1, P1, P2) along the northern margin of that ridge.

The results of DCA analyses using relative abundance codes (Text-fig. 10) suggest that, with the exception of locality E3 and three northern localities within the Lomas del Mar trend (LE1, P1, P2), the localities within the three better-sampled reef trends group together. The two clusters of localities within the Lomas del Mar trend are separated by a pronounced discontinuity; whereas localities within the Buenos Aires trend and Santa Rosa patch appear to overlap slightly. The Quebrada Chocolate locality is isolated in the plot of axis 1 vs. axis 2, but groups with the Buenos Aires locality in the plot of axis 1 vs. axis 3. These findings are consistent with those of the cluster analyses (Text-fig. 9).

Visual examination of the two DCA plots (Text-fig. 10) suggests that axis 1 corresponds with relative stratigraphic position and geologic age. Possible exceptions exist for locality E3 and the three northern localities within the Lomas del Mar trend. Nevertheless, older localities generally have high values along axis 1; whereas younger localities tend to have low values. DCA scores for species (Text-fig. 11) are also generally higher for extinct species than for living species along axis 1. In contrast, axes 2 and 3 appear to bear no relationship to stratigraphic position or to numbers of extinct vs. living species. Thus, axis 1 appears to be partially related to time; whereas axes 2 and 3 do not.

The distributions of branching, massive, and platy species along the three DCA axes (Text-fig. 11) suggest that: (1) on axis 1, platy species tend to have low values, branching species have high values, and massive species are more evenly distributed; (2) on axis 2, platy species tend to have high values, whereas branching and massive species have low values; and (3) on axis 3, platy, branching, and massive species are haphazardly scattered. These results suggest that environment may explain some of the variation along axes 1 and 2. The low values for platy species along axis 1 suggest that muddy or deep water conditions may be responsible for the tight cluster of Lomas del Mar localities on the extreme left sides of the plots in Text-figure 10. The low values for massive and branching species along axis 2 suggest that axis 2 may be more closely related to exposure and distance to shore, with more nearshore localities having low values. Unlike the other localities in the analysis, the two localities with the lowest values along axis 2 (BA1, BA4) are both *Porites* thickets, which today are most common in shallow nearshore areas. None of the three axes appear to be related to the number of specimens or species collected within each locality. Thus, both axes 1 and 2 appear to be somewhat related to the environment, but axis 3 does not.

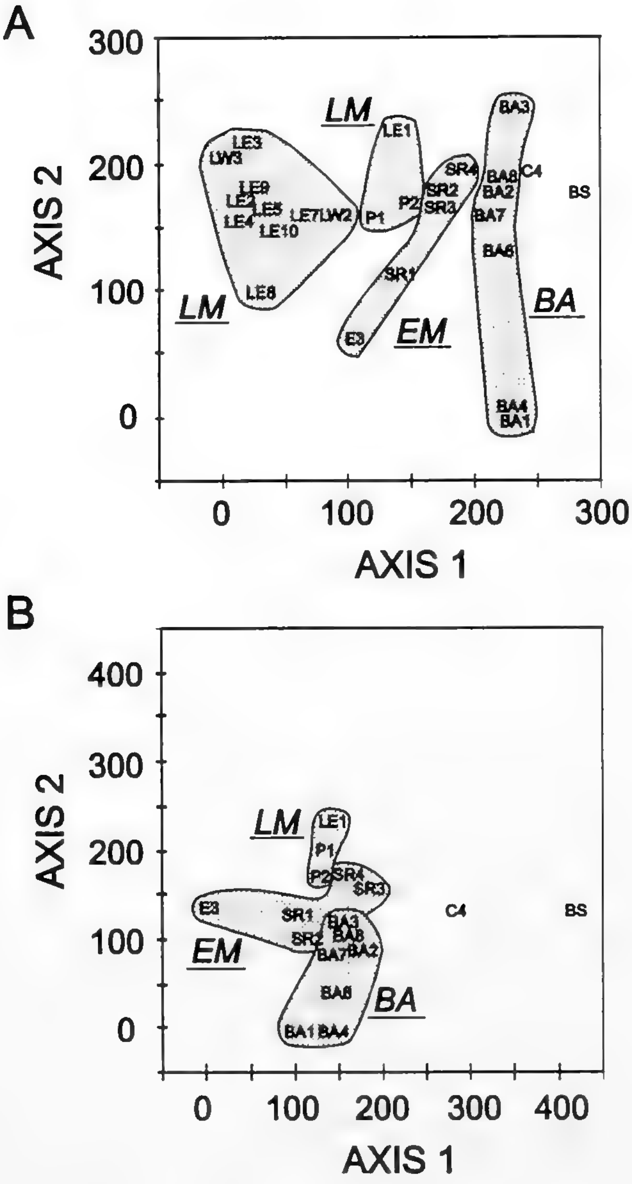
The distribution of localities along axis 1 in the DCA analysis based on binary data (Text-fig. 12a) is generally similar to that for relative abundances (Text-fig. 10). The main exceptions are: (1) the gap between



Text-figure 11.—Histograms of DCA scores for species determined using relative abundance code data. The analysis is the same as Text-fig. 10. Species are grouped by colony shape (left side) and by survivorship (right side). 'b', branching; 'm', massive; 'p', platy, 'E', extinct; 'L', living.

the two clusters of Lomas del Mar localities is less distinct, and (2) there is less overlap among the Santa Rosa and Buenos Aires localities. Even with these exceptions, axis 1 still appears to be related to time. The distribution of localities along axis 2, however, is somewhat different from the relative abundance results; the two stratigraphically older localities (BS, C4) no longer have relatively high values, localities with more massive species are no longer distinct from localities with more platy species, and the two localities in the Buenos Aires *Porites* thickets (BA1, BA4) are separated from the others by a large gap. Thus axis 2 appears to distinguish the two nearshore environments but is less clearly related to exposure. As in the relative abundance results, axis 3 is uninterpretable.

In order to better understand how the 10 tightly clustering localities from the Lomas del Mar trend affected the results, a final analysis was performed after these 10 localities were removed. The analysis was run using relative abundance codes. The results (Text-fig. 12b) show even stronger overlap among the Buenos Aires, Santa Rosa, and three remaining Lomas del Mar localities along axis 1 as well as considerable overlap among the Buenos Aires and Santa Rosa localities along axis 2. Thus, as in the cluster analysis results, the assemblages appear to intergrade, and although variation among assemblages appears to be coarsely related to evolution and environment, more refined relationships are difficult to decipher.



Text-figure 12.—Scatterplots of DCA scores for Costa Rican localities determined: (A) using binary data for 27 localities, (B) using relative abundance code data after the 10 tightly clustered localities in the Lomas del Mar trend were removed from the data set. Each point represents a locality, the abbreviations for which are given in Table 1. As in Text-figure 10, shaded areas encompass localities within the Buenos Aires (BA), Empalme (EM), and Lomas del Mar (LM) reef trends.

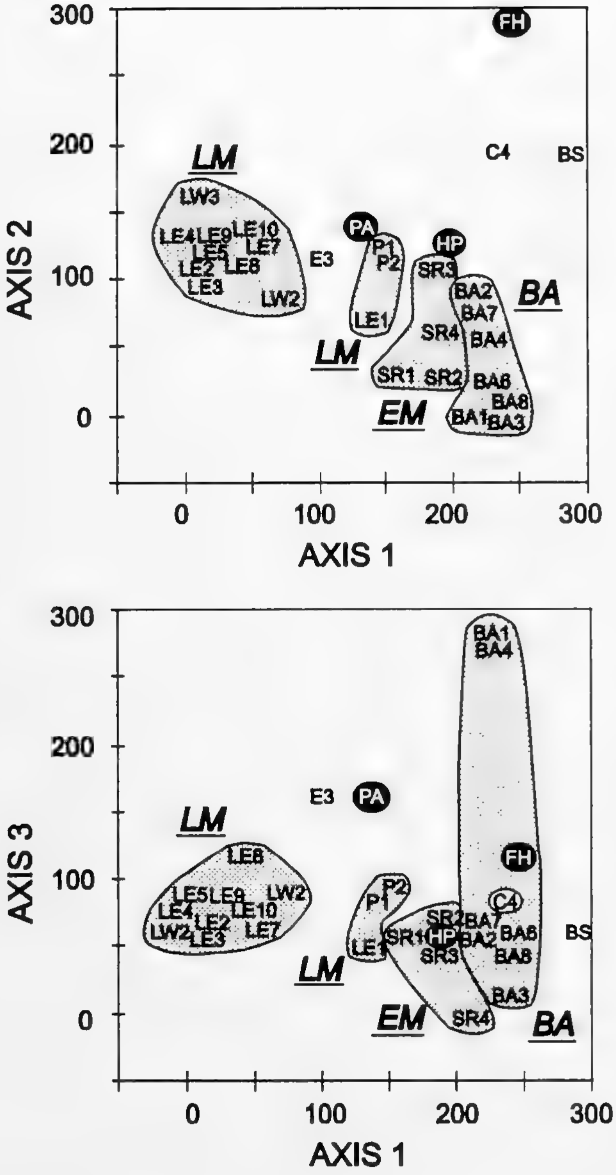
## PRELIMINARY COLLECTIONS FROM THE BOCAS DEL TORO REGION OF PANAMA

During August 1993, small collections of corals were made at seven sites in the Bocas del Toro region of Panama (Table 1; Appendix 1; Appendix A): five on Isla Colon (68 specimens, 26 species), one on Isla Bastimentos (21 specimens, 11 species), and one on Swan Cay (6 specimens, 6 species). Preliminary age estimates based on planktic foraminifera and nannofossils (Coates, this volume) are: 3.5–1.7 Ma for the sites on Isla Colon, 3.0–2.2 Ma for the site on Isla Bastimentos, and 1.6–1.2 Ma for the site on Swan Cay. Study of the 1:50000 Isla Colon (3744 III, Edicion 1-AMS, 1993) and the 1:50000 Bocas del Toro (3744 II, Edicion 1-AMS, 1993) topographic sheets and stratigraphic sections HP, FH, SC (Coates, this volume) indicates that the five sites on Isla Colon could be grouped into three localities: GC (PPP 1285), PA (PPP 1423, 1424), and HP (PPP 1260, 1425). Based on this grouping, five localities (HP, FH, SC, PA, GC) are represented in the Bocas del Toro collections (Table 1). Numbers of specimens collected per locality range from 6 to 32 (median = 21), and numbers of species collected per locality range from 2 to 18 (median = 11).

A total of 35 species (12 extinct, 23 living) belonging to 19 genera were identified in the Bocas del Toro collections (Table 3). Only one species [*Thysanus corbicula;* first occurrence = Chipola Fm, Florida (18–15 Ma), last occurrence = Old Pera Beds, Jamaica (2.5–1.8 Ma)], which occurred on Isla Bastimentos (FH), was recognized that was not found in the Limon collections. At the three Isla Colon localities, only two extinct branching species were found at Ground Creek (GC), 18 species (83.3% living) were found at Hill Point (HP), and 14 species (92.8% living) were found at Paunch (PA). In contrast, the fauna collected on Isla Bastimentos (FC) consisted of 11 species (27.2% living), and the collection made at Swan Cay (SC) contained 6 species (100% living). The fauna at Hill Point (HP) is distinctive among the Bocas del Toro collections in that it contains both *Acropora palmata* and species of *Stylophora.* The Isla Bastimentos fauna contains species of *Stylophora,* but lacks *Acropora.* The Swan Cay fauna contains only *Acropora palmata,* but lacks *Stylophora.* Thus, collections from Isla Bastimentos (FH) and Ground Creek (GC) consist primarily of the pre-turnover fauna, whereas those from Paunch (PA) and Swan Cay (SC) consist primarily of the post-turnover fauna. The Hill Point (HP) fauna consists of a mix of the pre- and post-turnover faunas.

Most of the species collected at Hill Point (HP) and Paunch (PA) had massive colony shapes; whereas those collected at Isla Bastimentos (FH) possessed a variety of branching, free-living, massive, and platy shapes. The small collection at Swan Cay (SC) contained species with branching, massive and platy shapes. The apparently high diversity at all but the Ground Creek (GC) locality suggests that the assemblages lived in open reef habitats, with the most exposed conditions occurring at Hill Point (HP) and Paunch (PA).

To further compare the Bocas del Toro assemblages



Text-figure 13.—Scatterplots of DCA scores for 27 Costa Rican and 3 Panamanian localities determined using relative abundance code data. Each point represents a locality, the abbreviations for which are given in Table 1. Panamanian localities are indicated by black dots. As in Text-figure 10, shaded areas encompass localities within the Buenos Aires (BA), Empalme (EM), and Lomas del Mar (LM) reef trends.

with the Limon assemblages, DCA was performed on the three Bocas del Toro localities with more than 10 specimens (HP, PA, FH) and the 27 Limon localities using relative abundance code data. Codes for the three Bocas del Toro assemblages (Table 7) were determined by the same methods as described above for the Limon analyses. The results (Text-fig. 13) reveal a similar configuration of clusters of Limon localities as found earlier for just the 27 Limon localities using relative abundance codes (Text-fig. 10). The Isla Bastimentos (FH) assemblage lies in an isolated portion of the axis 1 vs. axis 2 plot, closest to assemblages from the two older Limon reef trends (Quebrada Chocolate, Brazo Seco). It therefore can be interpreted as composed of a pre-turnover fauna that differs from the Limon pre-turnover fauna probably because of the environment. The Hill Point (HP) assemblage lies near the line of overlap between clusters of Buenos Aires trend localities and Santa Rosa patch localities, and appears to have a similar mixed pre- and post-turnover composition. The Paunch (PA) assemblage lies closest to the Empalme trend locality and the three northern localities within the Lomas del Mar trend. It therefore can be interpreted as composed of a post-turnover fauna in a shallow reef environment similar to portions of the Lomas del Mar trend.

## CONCLUSIONS

Our initial collecting efforts in the Limon and Bocas del Toro basins have clearly shown that coral reef communities were plentiful and diverse along the Caribbean coast of Costa Rica and Panama during the 1–3 million year interval of Plio-Pleistocene turnover in the reef coral fauna of the Caribbean region. In fact, the diversity of reef corals in the collected fossil assemblages exceeds that reported in the region today, as well as at other individual locations in the Caribbean during Plio-Pleistocene time. Although patchily distributed through geologic time, fossil assemblages in the two basins provide a wealth of data for exploring and comparing pathways of faunal replacement and community change.

In the Limon area, evidence for faunal change begins to appear between 3.6–3 Ma (the Quebrada Chocolate and Buenos Aires reef trends) and has almost ended by 1.9–1.6 Ma (the Empalme and Lomas del Mar trends). Similarly, in Curaçao, faunal change begins between 5.6–3 Ma and has almost ended by 2.6–2 Ma (Budd *et al.*, 1998), and in Jamaica, faunal change has ended in exposed shallow reef environments by 2–1.8 Ma (Budd and McNeill, 1998). In contrast, in Bocas del Toro, faunal change may not have begun until after 3–2.2 Ma in some places (*e.g.*, Isla Bastimentos), but was complete by 1.6–1.2 Ma (Swan Cay) or even earlier (Paunch). This delay in turnover has also been observed in protected reef margin environments in Jamaica (the Bowden-Old Pera sequence), in which faunal change did not begin until after 3.3–1.8 Ma (Budd and McNeill, 1998). These results indicate that the timing and pace of faunal change may have varied from place to place across the Caribbean region as a whole, and along the Caribbean coast of Costa Rica and Panama in particular. Transitional faunas in which extinct species of *Stylophora* and living species of *Acropora* co-occur can be found in both the Limon (Buenos Aires reef trend, 3.6–3 Ma) and Bocas del Toro (Hill Point, 3.5–1.7 Ma) areas, suggesting that faunal change may have occurred either gradually *or* in a series of steps in both areas.

To interpret the significance of these results, the observed patterns of faunal change need to be further refined, and to do this, clearly more samples need to be analyzed. In particular, large collections that are well-documented geographically, environmentally, and stratigraphically need to be collected at more sites throughout the Bocas del Toro area, and in Early Pliocene reefal deposits west of Limon. More precise environmental interpretations are needed for individual localities within trends to effectively tease apart the effects of environment and evolution in faunal analyses. Because examining co-occurrences of species has been found to be critical to understanding patterns of faunal change, the present analyses demonstrate the need for collections containing at least 50 specimens per site. Line transect or quadrat data documenting co-occurrences and relative abundances of species in the field, together with detailed taphonomic information, could further help to explain the variability in what preliminary results suggest to be a complex system. In addition, comparisons with patterns of change in other fossil groups could potentially assist in pinpointing and understanding the larger-scale external factors driving Plio-Pleistocene faunal change, as well as the apparently staggered and patchy response of reef communities to these factors.

In addition to tracing patterns of faunal change, our initial collections are, for the most part, exceptionally well-preserved, and contain many global first occurrences. They are therefore ideal for future morphometric studies of speciation in the fossil record, and for reconstructing phylogenies. For example, the two species of *Acropora* that dominate modern Caribbean reefs both have first occurrences in the Buenos Aires trend (McNeill *et al.*, 1997), and so do the oldest members of the equally important *Montastraea annularis* sibling species complex (Knowlton *et al.*, 1992). What was the pattern of speciation in these two clades, and what sort of morphologic innovations were involved? Did speciation within each clade involve an initial evolutionary burst or were speciation events staggered through time? What sorts of ecological conditions were associated with speciation? Collections such as those described herein provide an important starting point in searching for answers.

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# APPENDIX 1

## SPECIES OCCURRENCES

Species identified at PPP sites. Data are at the PPP internet site, http://www.fiu.edu/¯collinsl/.

| | 639 | 646 | 715 | 719 | 771 | 772 | 942 | 943 | 948 | 949 | 962 | 963 | 1100 | 1101 | 1102 | 1103 | 1104 | 1105 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Acropora cervicornis* | | 1 | | 2 | | 1 | | | | | | | | | | | | |
| *Acropora palmata* | | | | 2 | | | | | | | | | | | | | | |
| *Acropora* sp. | | | | | | | | | | | | | | | | | | |
| *Agaricia grahamae* | 3 | 25 | | | 1 | | 2 | 1 | | 1 | 20 | 8 | 1 | | 1 | 2 | 6 | 4 |
| *Agaricia lamarcki* | 3 | 9 | | | 1 | | 1 | 1 | | | 22 | 4 | 13 | | 1 | 2 | 1 | 1 |
| *Agaricia undata* | 1 | 9 | | | 1 | | 1 | | 1 | | 9 | 1 | 7 | | 2 | | 1 | 3 |
| *Antillia dentata* | | | | | | | | | | | | | | | | | | |
| *Antillophyllia sawkinsi* | | | | | | | | | | | | | 1 | | | | | |
| *Archohelia limonensis* | | | | | 1 | 1 | | | | | | | | | | | | |
| *Caulastraea portoricensis* | | | | 1 | | | | | | | | | | | | | | |
| *Colpophyllia amaranthus* | | | | 2 | | | | | | | | | | | | | | |
| *Colpophyllia natans* | | 1 | | 1 | | 1 | | 2 | | | 1 | | | 2 | | | | |
| *Colpophyllia* sp. A | | | | | | | | | | | | | | | | | | |
| *Dichocoenia caloosahatcheensis* | | | 1 | | | | | | | | | | | | | | | |
| *Dichocoenia eminens* | | | | | | | | | | | | | | | | | | |
| *Dichocoenia stokesi* | | 2 | 1 | 1 | | | | | | | | | 1 | | | | | |
| *Dichocoenia stellaris* | | 1 | | 1 | | | | 1 | | | 2 | 1 | | | 1 | | | |
| *Dichocoenia tuberosa* | | | | | | | | | | | | | | | | | | |
| *Diploria clivosa* | | | | | | | | | | | | | | | | | | |
| *Diploria labyrinthiformis* | | | | | | | | | | | | | | | | | | |
| *Diploria sarasotana* | | | | | | | | | | | | | | | | | | |
| *Diploria strigosa* | | | | 1 | | | | | | | | | | | | | | |
| *Eusmilia fastigiata* | | 1 | | 1 | | | 1 | | | | | | | | | | | |
| *Eusmilia* sp. A | | | | | | | | | | | | | | | | | | |
| *Favia fragum* | | | | | | | | | | | | | | | | | | |
| *Goniopora imperatoris* | | | | | | | | | | | | | | | | | | |
| *Helioseris cucullata* | 2 | 1 | | | | | | | | | 1 | | | | | | | |
| *Isophyllastrea* sp. B | | | | | | | | | | | | | | | | | | |
| *Madracis asperula* | | 1 | | | | | | | | | 2 | 3 | 4 | | | | | |
| *Madracis decactis* | | 4 | | | | | | | | | 4 | 29 | 1 | | 1 | 2 | 1 | 2 |
| *Madracis mirabilis* | 1 | 7 | 1 | 1 | 2 | 1 | 2 | 2 | | | 11 | 10 | | | 1 | | | |
| *Madracis pharensis* | | | | | | | | | | | | | 1 | | | | | |
| *Madracis* sp. A | | | | | | | 1 | | | | | | | | | | | |
| *Manicina areolata* | | 1 | | 1 | | | | | | | 3 | 2 | 1 | | | | | |
| *Manicina mayori* | | | | | | | 1 | | | | 1 | | | | | | 1 | |
| *Manicina puntagordensis* | | 2 | | | | | | | | | 3 | | 2 | | | | | |
| *Meandrina braziliensis* | | | | | | | | | | | | | | | | | | |
| *Meandrina meandrites* | | | | | | | 1 | | | | | | | | | | | |
| *Meandrina* sp. A | | | | 1 | | | | | | | | | | | | | | |
| *Millepora complanata* | | | | 1 | | | | | | | | | | | | | | |
| *Millepora* sp. | | | | 1 | | | | | | | | | | | | | | |
| *Montastraea canalis* | | 2 | | | | | | | | | 2 | | 1 | | | | | |
| *Montastraea cavernosa*-2 | 1 | | | | 1 | | | | | | | | | | | | | |
| *Montastraea cavernosa*-3 | | | | 1 | | | 1 | | | | 2 | | | | 1 | | | |
| *Montastraea cylindrica* | 1 | 4 | | 1 | | | 3 | 4 | | | 12 | 4 | | | 1 | 4 | 5 | |
| *Montastraea faveolata* | | | 1 | | | 1 | 1 | | | | | | | 1 | | | 1 | |
| *Montastraea franksi* | | | 1 | | | | | | | | | 1 | | | | | 1 | |
| *Montastraea limbata*-1 | | | | 1 | | | | | | | | | | | | | | |
| *Montastraea limbata*-2 | | 4 | | 2 | 1 | | 4 | 1 | 1 | | | | | | | | | |
| *Montastraea* sp. A | | | | 1 | | | | | | | | | | | | | | |
| *Mussa angulosa* | | | | | | | | | | | 1 | | | | | | | |
| *Mussismilia* aff. *M. hartti* | | | 1 | 1 | | | | | | | | | | | | | | |
| *Mycetophyllia aliciae* | | 1 | | | | | | | | | | | | | | | | |
| *Mycetophyllia danaana* | | | | | | | | 2 | | | 1 | | | 2 | | | | |
| *Mycetophyllia ferox* | | 1 | | | | | | 2 | | | | | | | | | | |
| *Mycetophyllia lamarckiana* | | | | | | | | | | | 1 | | | | | | | |
| *Mycetophyllia reesi* | 1 | 2 | | | | | | | | | 2 | 1 | | 1 | 1 | | | 2 |
| *Mycetophyllia* sp. A | | | | | | | | | | | | | | | | | | |
| *Pocillopora crassoramosa* | | | | | | | | | | | | | | | | | | |
| *Porites astreoides* | 1 | 1 | | 1 | | | | | | | | | | | | | | |
| *Porites baracoaensis* | | | | | | | | | | | | | | | | | | |
| *Porites branneri* | | 3 | 1 | | | 1 | 2 | 1 | | | 2 | | 1 | | | | 1 | |
| *Porites colonensis* | | 3 | | | | | | | | | 2 | 2 | | | | | | |
| *Porites furcata* | | | | 1 | 2 | 1 | | | | | | | | | | | | |
| *Porites porites* | | | | | | | | | | | | | | | | | | |
| *Porites portoricensis* | | | | | | | | | | | 2 | | | | | | | |
| *Porites waylandi* | | 1 | | | | | 1 | | | | | 1 | | | | | | |
| *Porites* sp. | | | | | | | | | | | | | | | | | | |
| *Placocyathus trinitatis* | | | | | | | | | | | | | | | | | | |
| *Placocyathus variabilis* | | 4 | | 1 | | | 1 | | | | 5 | | 3 | | | | 1 | |
| *Scolymia cubensis* | | 3 | | | | | | | | | 1 | 2 | | | | | | |
| *Scolymia lacera* | | 1 | | | | | | | | | | | | | | | | |
| *Siderastrea radians* | | | | | | 2 | | | | | | | | | | | | |
| *Siderastrea siderea* | 1 | 1 | 1 | 2 | 1 | | | | | | | | | | | | | |
| *Solenastrea bournoni* | | | | | 1 | | | | | | | | | | | | | |
| *Stephanocoenia intersepta* | 1 | 4 | 1 | | | | 2 | 3 | | | 8 | 3 | 1 | | 1 | | 1 | 2 |
| *Stephanocoenia duncani* | | 6 | 2 | 2 | | | 2 | 4 | | | 3 | 4 | 1 | 1 | 3 | 1 | | 3 |
| *Stephanocoenia spongiformis* | | | | | | | | | | | 2 | 1 | | | | | | 1 |
| *Stylophora affinis* | | | | | | | | | | | | | | | | | | |
| *Stylophora granulata* | | | | | | | | | | | | | | | | | | |
| *Stylophora minor* | | | | | | | | | | | | | | | | | | |
| *Stylophora monticulosa* | | | | | | | | | | | | | | | | | | |
| *Thysanus corbicula* | | | | | | | | | | | | | | | | | | |
| *Thysanus* sp. A | | | | | | | | | | | | | | | | | | |
| *Undaria agaricites* | 12 | 29 | 2 | 1 | 2 | 2 | 3 | 4 | | | 20 | 18 | 16 | | 6 | | 2 | 3 |
| *Undaria crassa* | | | | | 1 | 1 | | | | | | 1 | | | 1 | | | |
| *Undaria pusilla* | | | | | | | | | | | | | | | | | | |
| *Undaria* sp. | | | | | | | | | | | | | | | | | | |
| agariciid | | | | | | | | | | | | | | | | | | |
| Total specimens | 28 | 135 | 13 | 32 | 15 | 12 | 30 | 28 | 2 | 1 | 146 | 96 | 55 | 7 | 21 | 11 | 22 | 21 |

Appendix 1.—Continued.

| 1106 | 1107 | 1108 | 1109 | 1110 | 1111 | 1112 | 1113 | 1114 | 1115 | 1116 | 1117 | 1118 | 1119 | 1120 | 1121 | 1122 | 1123 | 1124 | 1125 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | | | | | | | | 3 | 3 |
| 1 | | | | | | | | | | | | | | | | | | 10 | 3 |
| 2 | 1 | | | | 2 | | | 2 | | | | 5 | 5 | 1 | 4 | 1 | 5 | | |
| 3 | 1 | | | | 1 | | | | | | | 2 | | | | | 2 | | |
| | 2 | | | | | | | | | | | 1 | | | | | 1 | | |
| | | | | | | | | | | | | | | | | | | 18 | |
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| 2 | 1 | 1 | 2 | | | | 3 | 3 | | 4 | 2 | 3 | 1 | | 1 | | 2 | | |
| 1 | | | | 1 | | | | 4 | | 1 | | 2 | 1 | | | 1 | | | |
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| | 1 | 1 | | 1 | | | 1 | | | | | | | | | 1 | | | |
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| | 3 | 2 | 5 | | | 1 | 5 | 2 | | 2 | 5 | 6 | 1 | 2 | | 2 | 2 | | |
| | | 2 | | | | 1 | 2 | 2 | | 2 | | | | 1 | 2 | | | | |
| | | | | | | | | | | | | 2 | 1 | | | | | 3 | |
| | | 1 | | | | | | | | | | | | | | | | 3 | |
| | | 1 | 1 | | 3 | 1 | | 1 | | 1 | | 1 | | 2 | | | | 8 | |
| | | | | | | | | | | | | | | | | | | 2 | |
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| 1 | 3 | 1 | 1 | 1 | | 1 | 3 | 1 | | | | 3 | 1 | 1 | 1 | | 1 | | |
| 4 | 4 | 2 | 3 | 1 | 3 | 3 | 2 | 5 | 1 | | 2 | 3 | 1 | 2 | 1 | 3 | 1 | | 1 |
| 1 | | | 1 | | | | | | | | 1 | | | | | | | | |
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| 5 | | 1 | 5 | 2 | 4 | 3 | 1 | 12 | | 1 | 3 | 9 | 7 | | 1 | 1 | 2 | 10 | |
| | | | | | | | | | | | | 1 | | | | | | | |
| 1 | | | | | | | | | | | | | | | | | | | |
| 22 | 17 | 15 | 21 | 8 | 14 | 11 | 19 | 38 | 1 | 12 | 15 | 42 | 18 | 11 | 15 | 12 | 18 | 94 | 19 |

Appendix 1.—Continued.

| | 1126 | 1127 | 1251 | 1260 | 1285 | 1310 | 1316 | 1331 | 1332 | 1333 | 1334 | 1335 | 1336 | 1337 | 1338 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Acropora cervicornis* | | 1 | | 1 | | | 7 | | | | | | 1 | | 1 |
| *Acropora palmata* | | 2 | | | | | | 1 | | | | 1 | 1 | | 1 |
| *Acropora* sp. | | | | | | | | | | | | | | | |
| *Agaricia grahamae* | | | | | | 3 | | | 2 | | | | | | |
| *Agaricia lamarcki* | | | | | | 2 | | | 2 | | 3 | | 1 | | |
| *Agaricia undata* | | | | | | 2 | | | 5 | | | | | | |
| *Antillia dentata* | | | | | | | | | | | | | | | |
| *Antillophyllia sawkinsi* | | | | | | | | | | | | | | | |
| *Archohelia limonensis* | | | | | | | | | | | | | | | |
| *Caulastraea portoricensis* | 1 | | | 3 | 1 | | 2 | 1 | | | | | | 1 | 1 |
| *Colpophyllia amaranthus* | | | | | | | 1 | | | | | | | | |
| *Colpophyllia natans* | | | | | | 1 | | 1 | | 1 | 2 | 3 | 1 | | |
| *Colpophyllia* sp. A | | 1 | | | | | | | | | 1 | 1 | | 1 | 2 |
| *Dichocoenia caloosahatcheensis* | | | | | | | | | | | | | | | |
| *Dichocoenia eminens* | | | 1 | | | | | | | | | | | | |
| *Dichocoenia stokesi* | | | | | | | | | | | | 1 | | | |
| *Dichocoenia stellaris* | | | | | | | | | | | | 1 | | | |
| *Dichocoenia tuberosa* | | | | | | 1 | | | | | | | | | |
| *Diploria clivosa* | | | | | | | | | | | | | | | |
| *Diploria labyrinthiformis* | | | | | | | | | | | | 2 | 2 | | |
| *Diploria sarasotana* | | | | | | | | | | | | | | | |
| *Diploria strigosa* | | 3 | 1 | | | | | | 1 | | 1 | 3 | 4 | | |
| *Eusmilia fastigiata* | | | | | | | | | | | | | | | |
| *Eusmilia* sp. A | 1 | | | 1 | | | | | 1 | | | | 1 | | |
| *Favia fragum* | | | | | | | | | | | | | | | |
| *Goniopora imperatoris* | | | | | | | | | | | | | | | |
| *Helioseris cucullata* | | | | | | | 3 | | | 2 | 1 | 1 | 1 | | |
| *Isophyllastrea* sp. B | | | | | | | | | | | | | | | |
| *Madracis asperula* | | | | | | 1 | | | | | | | | | |
| *Madracis decactis* | | 1 | | | | 3 | | | 2 | | | | | | |
| *Madracis mirabilis* | | | | | | | | | | | | | | | |
| *Madracis pharensis* | | | | | | | | | | | | | | | |
| *Madracis* sp. A | | | | | | | | | | | | | | | |
| *Manicina areolata* | | | | | | 1 | | | | | | | | | |
| *Manicina mayori* | 1 | 1 | | | | | | | | 1 | 2 | 1 | | | |
| *Manicina puntagordensis* | | | 1 | | | 2 | | | | | | | | | |
| *Meandrina braziliensis* | | | 3 | | | | | | | | | | | | |
| *Meandrina meandrites* | | | | | | 1 | | 1 | | | 1 | 1 | | | |
| *Meandrina* sp. A | | | | | | 1 | | | | 1 | 3 | | | | |
| *Millepora complanata* | | | | | | | | | | | | | | | |
| *Millepora* sp. | | | | | | | | | | | | | | | |
| *Montastraea canalis* | | | | | | | | | | | | | | 1 | |
| *Montastraea cavernosa*-2 | 1 | | | | | | 1 | | | 2 | 1 | 1 | 1 | | |
| *Montastraea cavernosa*-3 | | | | | | | | | | | | | | | |
| *Montastraea cylindrica* | | 1 | | | | 4 | | | 3 | | | | | | |
| *Montastraea faveolata* | | 3 | | | | 1 | | | | 2 | 2 | | 2 | 1 | 4 |
| *Montastraea franksi* | | | | | | 1 | 5 | 4 | | | 1 | 1 | | 1 | |
| *Montastraea limbata*-1 | | | | | | | | | | | | | | | |
| *Montastraea limbata*-2 | | 4 | 1 | | | 3 | | 1 | | | | | | 1 | |
| *Montastraea* sp. A | | | | | | | 5 | | | | | | | 1 | 1 |
| *Mussa angulosa* | | | | | | 1 | | | | | | | | | |
| *Mussismilia* aff. *M. hartti* | | | | | | | | 1 | 2 | | | | | | |
| *Mycetophyllia aliciae* | | | | | | | | | | | | | | | |
| *Mycetophyllia danaana* | | | | | | 1 | | | | 1 | | | 1 | | |
| *Mycetophyllia ferox* | | 2 | | | | 1 | | | | 1 | | | 1 | 1 | 1 |
| *Mycetophyllia lamarckiana* | | | | | | | | | | | | | | | |
| *Mycetophyllia reesi* | | | | | | 1 | | | | 1 | | | | | |
| *Mycetophyllia* sp. A | | | | | | | | | | | 2 | | | | |
| *Pocillopora crassoramosa* | | | 1 | | | | | | | | | | | | |
| *Porites astreoides* | | | | | | | 1 | | | 2 | 2 | 2 | 1 | 4 | 1 |
| *Porites baracoaensis* | | | | | 5 | | | 1 | | | | | | | |
| *Porites branneri* | | | | | | | | | 1 | | | | | | |
| *Porites colonensis* | | | | | | | | | | | | | | | |
| *Porites furcata* | | | | | | | 1 | 2 | 1 | | | | | | |
| *Porites porites* | | | | | | | | | | | | | | | |
| *Porites portoricensis* | | | | | | | 1 | 1 | | | | | | | |
| *Porites waylandi* | | | | | | | | | | | | | | | |
| *Porites* sp. | | | | | | | | | | | | | | | |
| *Placocyathus trinitatis* | | | | | | | | | | | | | | | |
| *Placocyathus variabilis* | | | 8 | | | 2 | | | 1 | | | | | | |
| *Scolymia cubensis* | | | | | | | | | | | | | | | |
| *Scolymia lacera* | | | | | | 1 | | | | | | | | | |
| *Siderastrea radians* | | | | | | | | | | | | | | | |
| *Siderastrea siderea* | | | | | | 1 | | | 1 | | 2 | | 1 | | |
| *Solenastrea bournoni* | | | | | | | | | | 2 | 1 | | | | |
| *Stephanocoenia intersepta* | | | | | | 4 | | | 2 | | | | 1 | | |
| *Stephanocoenia duncani* | | | 1 | | | 2 | 1 | | 4 | | | | 2 | | |
| *Stephanocoenia spongiformis* | | | | | | | | | | | | | | | |
| *Stylophora affinis* | | | | 1 | | | | | | | | | | | |
| *Stylophora granulata* | | | | 4 | | | 4 | | | | | | | | |
| *Stylophora minor* | | | | | | | | | | | | | | | |
| *Stylophora monticulosa* | | | 2 | | | | 1 | | | | | | | | |
| *Thysanus corbicula* | | | 1 | | | | | | | | | | | | |
| *Thysanus* sp. A | 1 | | | | | | 1 | 1 | | | | | | | |
| *Undaria agaricites* | | 16 | 1 | 2 | | 4 | 7 | 1 | 5 | 1 | 5 | 1 | 1 | | |
| *Undaria crassa* | | | | | | | | | | 2 | | 2 | 3 | 1 | 1 |
| *Undaria pusilla* | | | | | | | | | | | | | | 1 | |
| *Undaria* sp. | | | | | | | | | | | | | | | |
| agariciid | | | | | | | | | | | | | | | |
| Total specimens | 5 | 35 | 21 | 12 | 6 | 45 | 41 | 16 | 33 | 19 | 30 | 22 | 26 | 14 | 13 |

Appendix 1.—Continued.

| 1339 | 1340 | 1341 | 1342 | 1343 | 1344 | 1345 | 1346 | 1347 | 1348 | 1349 | 1350 | 1351 | 1352 | 1353 | 1355 | 1357 | 1358 | 1359 | 1360 | 1362 |
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| | | 4 | 10 | 4 | 3 | | 2 | | | | | 1 | | | | | | | | 2 |
| | | 3 | 3 | 1 | 2 | | | | | | | | | 1 | 1 | | | | | |
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| 1 | 1 | 1 | 2 | 1 | 4 | | 1 | | 1 | 1 | | | | | | | | | | |
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| | | 1 | 5 | 1 | 4 | 1 | 1 | | | | | 2 | | | | | | | | |
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| 1 | 1 | | 1 | | 9 | 1 | | | 1 | | 2 | 3 | 1 | | | | | | | |
| | | 1 | 1 | 3 | 3 | 1 | 1 | | 3 | | | | 1 | | | | | | | |
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| | | | 1 | 1 | 3 | | | 1 | 1 | | | | | | | | | 1 | 1 | 1 |
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| | | | 1 | 1 | | | | | 1 | | | | | | | | | | | |
| | | 1 | 1 | 3 | 3 | | 2 | 1 | 6 | 4 | | 5 | | 2 | | 2 | 3 | 1 | | 1 |
| 2 | | 1 | 1 | | 1 | | | | | | | | | | | | | | | |
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| 5 | 4 | 21 | 35 | 21 | 69 | 9 | 9 | 3 | 20 | 12 | 2 | 36 | 6 | 7 | 4 | 9 | 13 | 6 | 1 | 9 |

Appendix 1.—Continued.

| | 1363 | 1364 | 1365 | 1366 | 1367 | 1370 | 1372 | 1373 | 1374 | 1375 | 1381 | 1384 | 1385 | 1386 | 1387 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Acropora cervicornis* | | | | 3 | 2 | | | 3 | | | | 4 | | 2 | |
| *Acropora palmata* | | 1 | | 2 | 3 | | 3 | | | | | | | | |
| *Acropora* sp. | | | | | | | | | | | 1 | | | | |
| *Agaricia grahamae* | | | | | | | | | | 3 | | | | | |
| *Agaricia lamarcki* | | | | | | | | | | | | 1 | 1 | | |
| *Agaricia undata* | | | | | | | | | | 1 | | | 1 | | |
| *Antillia dentata* | | | | | | | | | | | | | | | |
| *Antillophyllia sawkinsi* | | | | | | | | | | | | | | | |
| *Archohelia limonensis* | | | | | | | | | | | | | | | |
| *Caulastraea portoricensis* | | | | 4 | 3 | | 3 | 3 | 1 | 1 | | | | | |
| *Colpophyllia amaranthus* | | | | | | | | | | | | | | | |
| *Colpophyllia natans* | | | | | | | | | 4 | | | 1 | | | |
| *Colpophyllia* sp. A | | | | | | | | 1 | | | | | | | |
| *Dichocoenia caloosahatcheensis* | | | | | | | | | | | | | | | |
| *Dichocoenia eminens* | | | | | | | | | | | | 1 | | | |
| *Dichocoenia stokesi* | | | 1 | 2 | | | | 3 | | | | 1 | | | |
| *Dichocoenia stellaris* | | | | | 1 | | | | | | | | | | |
| *Dichocoenia tuberosa* | | | | | | | | | | | 2 | 1 | | | |
| *Diploria clivosa* | | | | | 1 | | 1 | | | | 2 | | | | |
| *Diploria labyrinthiformis* | | | | 2 | | | | | 3 | | | | | | |
| *Diploria sarasotana* | | | | | | | 1 | | | | | | | | |
| *Diploria strigosa* | | | | | 3 | | 1 | | 1 | | | | | | |
| *Eusmilia fastigiata* | | | | | | | | | | | | | | | |
| *Eusmilia* sp. A | | | | | | | | | | | | 5 | | | |
| *Favia fragum* | | | | 1 | | | | | | | | 1 | | | 1 |
| *Goniopora imperatoris* | | | | | | | | | | | | | | 1 | |
| *Helioseris cucullata* | | | | | | | | | | | 4 | 1 | | | |
| *Isophyllastrea* sp. B | | | | | | | | | | | | | | | |
| *Madracis asperula* | | | | | | | | | | | | | 1 | | |
| *Madracis decactis* | | | | | | | | 2 | | | 1 | | | | |
| *Madracis mirabilis* | | | | | | | | | | | | | 1 | | |
| *Madracis pharensis* | | | | | | | | | | | | | | | |
| *Madracis* sp. A | | | | | | | | | | | 2 | 1 | | | |
| *Manicina areolata* | | | | 3 | | | 2 | 1 | | | | | | | |
| *Manicina mayori* | | | | 1 | 1 | | | | | | | 1 | | | |
| *Manicina puntagordensis* | | | | 1 | | | | | | | 1 | | | | |
| *Meandrina braziliensis* | | | | | | | | | | | 1 | | | | |
| *Meandrina meandrites* | | | | | | | | | 1 | | | | | | |
| *Meandrina* sp. A | | | | | | | | | | | | | | | |
| *Millepora complanata* | | | | | | | | | | | | 1 | | | |
| *Millepora* sp. | | | | | | | | 1 | | | | | | | |
| *Montastraea canalis* | | | | | 1 | | | | | | | | 1 | | |
| *Montastraea cavernosa*-2 | | | | | | | 1 | 1 | 2 | | | 3 | | | |
| *Montastraea cavernosa*-3 | | | | | | | | | 1 | | | | | | |
| *Montastraea cylindrica* | | | | | | | | | 1 | 1 | | | | | |
| *Montastraea faveolata* | | | | | | | 1 | | | | | | 1 | | |
| *Montastraea franksi* | | | 1 | | | | | | | | | 1 | | | |
| *Montastraea limbata*-1 | | | | 2 | | | | | | | | | | | |
| *Montastraea limbata*-2 | | | | 1 | | | 1 | | | | | 2 | | | |
| *Montastraea* sp. A | | | | | 2 | | 1 | | 1 | | 3 | 1 | | | |
| *Mussa angulosa* | | | | | | | | | | | | | | | |
| *Mussismilia* aff. *M. hartti* | | | | | | | | | | | | | | | |
| *Mycetophyllia aliciae* | | | | | | | | | | | | | | | |
| *Mycetophyllia danaana* | | | | | | | | | | | | | | | |
| *Mycetophyllia ferox* | | | | | | | | | | | | | | | |
| *Mycetophyllia lamarckiana* | | | | | | | | | | | | | | | |
| *Mycetophyllia reesi* | | | | | | | | | | | | | | | |
| *Mycetophyllia* sp. A | | | | | | | | | | | | | | | |
| *Pocillopora crassoramosa* | | | | | | | | | | | 17 | 1 | | 1 | |
| *Porites astreoides* | | | | | 2 | | 1 | 1 | 3 | | | | | 1 | |
| *Porites baracoaensis* | | 2 | | 3 | | | | | | | 1 | 1 | | 2 | 2 |
| *Porites branneri* | | | | | | | | | | | | | | | |
| *Porites colonensis* | | | | | | | | | | | | | | | |
| *Porites furcata* | 2 | 2 | | 6 | | 2 | | 5 | | | | | | | 6 |
| *Porites porites* | | | | | | | | 1 | | | | | | | |
| *Porites portoricensis* | | | | | | | | | | | | 2 | | | 1 |
| *Porites waylandi* | | | | | | | | | | | | 1 | | | |
| *Porites* sp. | | 1 | | | | | | | | | | | | | |
| *Placocyathus trinitatis* | | | | | | | | | | | 2 | | | | |
| *Placocyathus variabilis* | | | | | | | | | | | 7 | 1 | 1 | | |
| *Scolymia cubensis* | | | | | | | | | | | | | | | |
| *Scolymia lacera* | | | | | | | | | | | | | | | |
| *Siderastrea radians* | | | | | | | | | | | | | | | |
| *Siderastrea siderea* | | | | | 1 | | | 6 | | | 1 | 1 | | 3 | |
| *Solenastrea bournoni* | | | | | | | | | | | 3 | 9 | | | |
| *Stephanocoenia intersepta* | | | | | | | | | | 1 | | | 1 | | |
| *Stephanocoenia duncani* | | | | | 1 | | | 3 | | | | 5 | 1 | | |
| *Stephanocoenia spongiformis* | | | | | | | | | | | | | | | |
| *Stylophora affinis* | | | | | | | | | | | | 2 | | | |
| *Stylophora granulata* | | | | | | | | | | | | | | | |
| *Stylophora minor* | | | | | | | | | | | 4 | 2 | | | |
| *Stylophora monticulosa* | | | | | | | | | | | 1 | 2 | | | |
| *Thysanus corbicula* | | | | | | | | | | | | | | | |
| *Thysanus* sp. A | | | | 3 | | | | 1 | | | | 3 | | | |
| *Undaria agaricites* | | | | 1 | | | 1 | 2 | | | 1 | 8 | 3 | | |
| *Undaria crassa* | | | | | 2 | | 2 | | | | 2 | 2 | | | |
| *Undaria pusilla* | | | | | | | 1 | | | | 1 | | | | |
| *Undaria* sp. | | | | | | | | | | | | | | | |
| agariciid | | | | | | | | | | | | | | | |
| Total specimens | 2 | 6 | 2 | 35 | 23 | 2 | 20 | 34 | 18 | 7 | 57 | 66 | 12 | 10 | 10 |

Appendix 1.—Continued.

| 1388 | 1389 | 1390 | 1410 | 1412 | 1413 | 1414 | 1415 | 1416 | 1423 | 1424 | 1425 | 1426 | 1427 | 1428 | 1499 | 1500 | 1971 | 1972 | 2002 |
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| 14 | | | | | | | | | | | | 1 | 1 | | | | | | |
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| | 6 | | | | 1 | 4 | 2 | 1 | | | | | | | | | 2 | 2 | |
| | 6 | | 1 | | 1 | 1 | 1 | 1 | | | | | | | | | 2 | 2 | |
| | 5 | | 1 | | 1 | | 1 | 1 | | | | | | | | | 1 | 1 | |
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| 3 | 1 | | | 1 | | 1 | | | 5 | | 1 | | | | | 1 | | | |
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| | 6 | | 2 | | 1 | 1 | 1 | 3 | | | 1 | | | | | | 2 | 2 | |
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| | | 1 | | | | | | | | | | | | 3 | | | | | |
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| | 5 | | 3 | 2 | 1 | | 1 | 3 | | | | | | | | | 1 | 1 | |
| | 1 | | | | | | | | 2 | 1 | 2 | | | | | | 3 | 3 | 1 |
| 7 | 1 | 1 | | | | | | | 1 | | | 1 | 1 | | | | 1 | 1 | |
| | | | | | | | | | | | | | | | | | | | |
| 1 | 4 | | | 3 | 1 | | | 2 | | | | | | 1 | 2 | 2 | | | |
| 1 | | | | | | | | | | | | | | | | | 1 | 1 | |
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| | 1 | | 1 | 1 | 1 | | 1 | | | | | | | | | | | | |
| 3 | | | | | | | | | | | | 3 | 3 | | 4 | | | | 1 |
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| | 3 | | 1 | | | | 3 | 1 | | | | | | | | | 3 | 3 | |
| | 2 | | | 3 | | 1 | 1 | | 1 | | | | | | | | 1 | 1 | |
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| | | | | | | | | | | | | | | | 1 | | | | |
| 2 | 5 | 3 | 1 | 1 | 5 | 3 | 1 | 2 | 2 | | 1 | | | 2 | 2 | | 3 | 3 | 1 |
| | | | | | | | | | | | 1 | | | | | | | | |
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| | | | | | | | | | 1 | | | | | | | | | | |
| 37 | 63 | 11 | 11 | 15 | 14 | 14 | 19 | 24 | 28 | 5 | 18 | 9 | 9 | 9 | 17 | 12 | 24 | 24 | 6 |

Appendix 1.—Continued.

| | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 |
|---|---|---|---|---|---|---|---|
| *Acropora cervicornis* | | | | | | | |
| *Acropora palmata* | | | | | | | |
| *Acropora* sp. | | | | | | | |
| *Agaricia grahamae* | 1 | 1 | | | 1 | 2 | 4 |
| *Agaricia lamarcki* | 1 | 2 | | | 1 | | |
| *Agaricia undata* | 1 | | | 1 | 1 | 1 | 1 |
| *Antillia dentata* | | | | | | | |
| *Antillophyllia sawkinsi* | | | | | | | |
| *Archohelia limonensis* | | | | | | | |
| *Caulastraea portoricensis* | | | | | | | |
| *Colpophyllia amaranthus* | | | | | | | |
| *Colpophyllia natans* | | 1 | | | | | 1 |
| *Colpophyllia* sp. A | 1 | | | | 1 | | |
| *Dichocoenia caloosahatcheensis* | | | | | | | |
| *Dichocoenia eminens* | | | | | | | |
| *Dichocoenia stokesi* | | | | | | | |
| *Dichocoenia stellaris* | | | | | | | |
| *Dichocoenia tuberosa* | 1 | | | | | | |
| *Diploria clivosa* | | | | | | | |
| *Diploria labyrinthiformis* | | | | | | | |
| *Diploria sarasotana* | | | | | | | |
| *Diploria strigosa* | | | | | | | |
| *Eusmilia fastigiata* | | | | | | 1 | 1 |
| *Eusmilia* sp. A | | | | | | | |
| *Favia fragum* | | | | | | | |
| *Goniopora imperatoris* | | | | | | | |
| *Helioseris cucullata* | | 1 | | | | | |
| *Isophyllastrea* sp. B | | | | | | | |
| *Madracis asperula* | | 2 | 1 | 1 | 1 | | 1 |
| *Madracis decactis* | 2 | 2 | 1 | 2 | 1 | 2 | 3 |
| *Madracis mirabilis* | | | | | 1 | | |
| *Madracis pharensis* | | | | | | | |
| *Madracis* sp. A | | | | | | | |
| *Manicina areolata* | 1 | | | | | | 1 |
| *Manicina mayori* | 1 | 2 | | | | | |
| *Manicina puntagordensis* | | 2 | | 1 | | | |
| *Meandrina braziliensis* | | | | | | | |
| *Meandrina meandrites* | | | | | | | |
| *Meandrina* sp. A | | | | | | | |
| *Millepora complanata* | | | | | | | |
| *Millepora* sp. | | | | | | | |
| *Montastraea canalis* | | | | | | | |
| *Montastraea cavernosa*-2 | | | | | | | |
| *Montastraea cavernosa*-3 | | | | | | | |
| *Montastraea cylindrica* | 2 | 1 | 1 | 1 | 2 | | 1 |
| *Montastraea faveolata* | | | | | | | |
| *Montastraea franksi* | | | | | | | |
| *Montastraea limbata*-1 | | | | | | | |
| *Montastraea limbata*-2 | | 1 | | | | | |
| *Montastraea* sp. A | | | | | | | |
| *Mussa angulosa* | | | | | | | |
| *Mussismilia* aff. *M. hartti* | | | | | | | |
| *Mycetophyllia aliciae* | | | | | | | |
| *Mycetophyllia danaana* | 1 | | | | | | |
| *Mycetophyllia ferox* | | | | | | | |
| *Mycetophyllia lamarckiana* | | | | | | | |
| *Mycetophyllia reesi* | 3 | | | | | | 2 |
| *Mycetophyllia* sp. A | | | | | | | |
| *Pocillopora crassoramosa* | | | | | | | |
| *Porites astreoides* | | 1 | | | | 1 | |
| *Porites baracoaensis* | | | | | | | |
| *Porites branneri* | | 1 | | | | | |
| *Porites colonensis* | | | | | | | |
| *Porites furcata* | | | | | | | |
| *Porites porites* | | | | | | | |
| *Porites portoricensis* | | | | | | | |
| *Porites waylandi* | | | | | | | |
| *Porites* sp. | | | | | | | |
| *Placocyathus trinitatis* | | | | | | | |
| *Placocyathus variabilis* | 1 | 1 | 1 | | 1 | | |
| *Scolymia cubensis* | | | | | | | |
| *Scolymia lacera* | | | | | | | |
| *Siderastrea radians* | | | | | | | |
| *Siderastrea siderea* | | | | 1 | 1 | 1 | |
| *Solenastrea bournoni* | | | | | | | |
| *Stephanocoenia intersepta* | | | | | | | 3 |
| *Stephanocoenia duncani* | | 1 | 1 | 2 | 1 | | |
| *Stephanocoenia spongiformis* | 1 | | | | | | |
| *Stylophora affinis* | | | | | | | |
| *Stylophora granulata* | | | | | | | |
| *Stylophora minor* | | | | | | | |
| *Stylophora monticulosa* | | | | | | | |
| *Thysanus corbicula* | | | | | | | |
| *Thysanus* sp. A | | | | | | | |
| *Undaria agaricites* | 1 | 5 | 1 | 1 | 3 | 1 | 3 |
| *Undaria crassa* | | | | | | | |
| *Undaria pusilla* | | | | | | | |
| *Undaria* sp. | | | | | | | |
| agariciid | | | | | | | |
| Total specimens | 18 | 24 | 6 | 10 | 15 | 9 | 21 |

## CHAPTER 8

# NEOGENE CHEILOSTOME BRYOZOA OF TROPICAL AMERICA: COMPARISON AND CONTRAST BETWEEN THE CENTRAL AMERICAN ISTHMUS (PANAMA, COSTA RICA) AND THE NORTH-CENTRAL CARIBBEAN (DOMINICAN REPUBLIC)

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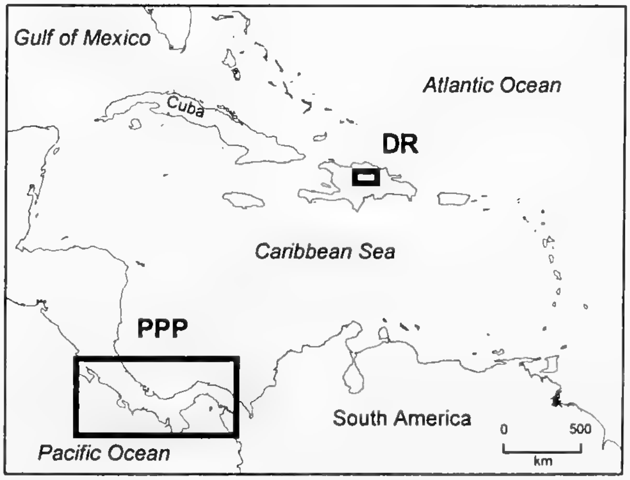
## INTRODUCTION

The Neogene (Miocene–Pleistocene) deposits of tropical America have long been known to contain a rich fossil record of cheilostome Bryozoa (Canu and Bassler, 1918, 1919, 1923, 1928), but detailed quantitative study of its diversity, spatial and temporal distribution, and evolutionary significance has only recently become possible. Extensive collections (Text-fig. 1) from detailed stratigraphic sequences in Panama and Costa Rica (Panama Paleontology Project, PPP; Coates *et al.*, 1992; Jackson *et al.*, 1996; Coates, this volume), and from the Dominican Republic (DR; Saunders *et al.*, 1982; Saunders *et al.*, 1986) provide a new basis for this undertaking. The opportunity now exists to document species ranges in space and time more precisely, and thus to explore the relationships between the cheilostome fauna and major environmental changes, such as those associated with the shoaling and final emergence of the Central American isthmus and closure of the isthmian seaway (Duque-Caro,



Text-figure 1.—Sketch map of the Caribbean and adjacent areas showing general locations of the PPP and DR collecting sites.

Table 1.—Diversity and abundance of cheilostome bryozoans (total and by growth form) in Panama Paleontology Project (PPP) collections containing six or more species each.

| Collection number | Age (Ma) | Paleodepth (m) | Number of species | | | | Abundance | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Total | Encrusting | Erect | Free-living | Total | Encrusting | Erect | Free-living |
| Canal Basin | | | | | | | | | | |
| PPP 222 | 11.6 | 27.5 | 6 | 6 | 0 | 0 | 15 | 15 | 0 | 0 |
| PPP 35 | 9.6 | 27.5 | 8 | 2 | 6 | 0 | 35 | 2 | 33 | 0 |
| PPP 162 | 8.6 | 25.0 | 22 | 13 | 2 | 7 | 40 | 13 | 2 | 25 |
| Bocas del Toro Basin | | | | | | | | | | |
| PPP 391 | 5.7 | 150.0 | 9 | 4 | 1 | 4 | 18 | 4 | 1 | 13 |
| PPP 60 | 4.3 | 60.0 | 9 | 6 | 1 | 2 | 9 | 6 | 1 | 2 |
| PPP 201 | 4.3 | 60.0 | 6 | 1 | 0 | 5 | 15 | 1 | 0 | 14 |
| PPP 203 | 4.3 | 42.5 | 8 | 2 | 0 | 6 | 251 | 11 | 0 | 240 |
| PPP 204 | 4.3 | 42.5 | 16 | 9 | 0 | 7 | 169 | 18 | 0 | 151 |
| PPP 205 | 4.3 | 42.5 | 28 | 20 | 1 | 7 | 271 | 47 | 1 | 223 |
| PPP 206 | 4.3 | 42.5 | 21 | 13 | 2 | 6 | 471 | 58 | 2 | 411 |
| PPP 207 | 4.3 | 42.5 | 14 | 6 | 1 | 7 | 527 | 6 | 1 | 520 |
| PPP 208 | 4.3 | 42.5 | 7 | 1 | 0 | 6 | 241 | 1 | 0 | 240 |
| PPP 419 | 4.3 | 50.0 | 7 | 2 | 0 | 5 | 34 | 11 | 0 | 23 |
| PPP 422 | 4.3 | 50.0 | 13 | 5 | 1 | 7 | 166 | 5 | 1 | 160 |
| PPP 423 | 4.3 | 50.0 | 8 | 0 | 1 | 7 | 152 | 0 | 10 | 142 |
| PPP 425 | 4.3 | 50.0 | 6 | 0 | 0 | 6 | 51 | 0 | 0 | 51 |
| PPP 426 | 4.3 | 50.0 | 6 | 0 | 0 | 6 | 420 | 0 | 0 | 420 |
| PPP 64 | 3.6 | 60.0 | 14 | 7 | 2 | 5 | 41 | 7 | 2 | 32 |
| PPP 65 | 3.6 | 60.0 | 45 | 29 | 7 | 9 | 243 | 74 | 16 | 153 |
| PPP 66 | 3.6 | 60.0 | 33 | 23 | 2 | 8 | 627 | 23 | 2 | 602 |
| PPP 67 | 3.6 | 60.0 | 14 | 6 | 0 | 8 | 617 | 6 | 0 | 611 |
| PPP 294 | 3.6 | 60.0 | 25 | 15 | 2 | 8 | 97 | 15 | 2 | 80 |
| PPP 295 | 3.6 | 60.0 | 28 | 16 | 4 | 8 | 415 | 52 | 13 | 350 |
| PPP 298 | 3.6 | 60.0 | 27 | 15 | 4 | 8 | 432 | 60 | 22 | 350 |
| PPP 306 | 3.6 | 60.0 | 14 | 6 | 0 | 8 | 356 | 6 | 0 | 350 |
| PPP 307 | 3.6 | 60.0 | 20 | 11 | 1 | 8 | 443 | 20 | 1 | 422 |
| PPP 308 | 3.6 | 60.0 | 25 | 14 | 1 | 10 | 583 | 50 | 1 | 532 |
| PPP 311 | 3.6 | 60.0 | 9 | 3 | 0 | 6 | 234 | 3 | 0 | 231 |
| PPP 312 | 3.6 | 60.0 | 13 | 5 | 2 | 6 | 40 | 5 | 2 | 33 |
| PPP 326 | 3.6 | 60.0 | 16 | 8 | 2 | 6 | 52 | 8 | 2 | 42 |
| PPP 334 | 3.6 | 60.0 | 27 | 14 | 4 | 9 | 531 | 167 | 22 | 342 |
| PPP 335 | 3.6 | 60.0 | 20 | 10 | 1 | 9 | 191 | 37 | 1 | 153 |
| PPP 340 | 3.6 | 60.0 | 25 | 13 | 3 | 9 | 234 | 51 | 3 | 180 |
| PPP 341 | 3.6 | 60.0 | 16 | 6 | 2 | 8 | 74 | 17 | 2 | 55 |
| PPP 345 | 3.6 | 42.5 | 19 | 9 | 3 | 7 | 109 | 27 | 12 | 70 |
| PPP 346 | 3.6 | 42.5 | 18 | 8 | 3 | 7 | 81 | 17 | 3 | 61 |
| PPP 348 | 3.6 | 42.5 | 19 | 7 | 3 | 9 | 91 | 16 | 12 | 63 |
| PPP 349 | 3.6 | 42.5 | 14 | 2 | 4 | 8 | 77 | 2 | 13 | 62 |
| PPP 350 | 3.6 | 42.5 | 29 | 14 | 4 | 11 | 677 | 113 | 22 | 542 |
| PPP 352 | 3.6 | 42.5 | 40 | 27 | 3 | 10 | 751 | 189 | 12 | 550 |
| PPP 354 | 3.6 | 42.5 | 13 | 6 | 1 | 6 | 40 | 6 | 1 | 33 |
| PPP 355 | 3.6 | 42.5 | 16 | 7 | 2 | 7 | 439 | 7 | 2 | 430 |
| PPP 357 | 3.6 | | 11 | 1 | 1 | 9 | 164 | 1 | 1 | 162 |
| PPP 365 | 3.6 | 125.0 | 12 | 1 | 4 | 7 | 75 | 10 | 13 | 52 |
| PPP 367 | 3.6 | 125.0 | 27 | 11 | 7 | 9 | 342 | 56 | 16 | 270 |
| PPP 368 | 3.6 | 125.0 | 24 | 9 | 4 | 11 | 114 | 18 | 13 | 83 |
| PPP 370 | 3.6 | 125.0 | 19 | 6 | 4 | 9 | 190 | 15 | 4 | 171 |
| PPP 53 | 3.5 | | 7 | 1 | 2 | 4 | 16 | 10 | 2 | 4 |
| PPP 55 | 3.5 | | 8 | 4 | 0 | 4 | 26 | 22 | 0 | 4 |
| PPP 57 | 3.5 | 30.0 | 10 | 0 | 1 | 9 | 154 | 0 | 1 | 153 |
| PPP 63 | 3.5 | 30.0 | 11 | 4 | 1 | 6 | 236 | 4 | 1 | 231 |
| PPP 68 | 3.5 | | 48 | 23 | 15 | 10 | 1488 | 482 | 285 | 721 |
| PPP 69 | 3.5 | | 36 | 21 | 5 | 10 | 1107 | 273 | 113 | 721 |

Table 1.—Continued.

| Collection number | Age (Ma) | Paleodepth (m) | Number of species | | | | Abundance | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Total | Encrusting | Erect | Free-living | Total | Encrusting | Erect | Free-living |
| PPP 71 | 3.5 | | 7 | 1 | 0 | 6 | 25 | 1 | 0 | 24 |
| PPP 72 | 3.5 | | 7 | 0 | 1 | 6 | 52 | 0 | 1 | 51 |
| PPP 74 | 3.5 | | 12 | 1 | 2 | 9 | 345 | 10 | 2 | 333 |
| PPP 193 | 3.5 | 30.0 | 11 | 3 | 1 | 7 | 344 | 3 | 10 | 331 |
| PPP 194 | 3.5 | 30.0 | 14 | 5 | 1 | 8 | 365 | 5 | 10 | 350 |
| PPP 195 | 3.5 | 30.0 | 9 | 1 | 1 | 7 | 315 | 1 | 1 | 313 |
| PPP 196 | 3.5 | 30.0 | 10 | 4 | 0 | 6 | 46 | 4 | 0 | 42 |
| PPP 197 | 3.5 | 30.0 | 8 | 1 | 1 | 6 | 53 | 1 | 10 | 42 |
| PPP 198 | 3.5 | 30.0 | 18 | 7 | 1 | 10 | 380 | 16 | 10 | 354 |
| PPP 210 | 3.5 | | 45 | 23 | 13 | 9 | 873 | 365 | 247 | 261 |
| PPP 211 | 3.5 | | 20 | 8 | 10 | 2 | 263 | 17 | 136 | 110 |
| PPP 212 | 3.5 | | 31 | 15 | 8 | 8 | 445 | 60 | 35 | 350 |
| PPP 379 | 3.5 | 175.0 | 9 | 3 | 0 | 6 | 63 | 3 | 0 | 60 |
| PPP 358 | 2.8 | 125.0 | 7 | 1 | 1 | 5 | 25 | 1 | 1 | 23 |
| PPP 361 | 2.8 | 125.0 | 8 | 3 | 1 | 4 | 35 | 3 | 10 | 22 |
| PPP 362 | 2.8 | 125.0 | 18 | 4 | 2 | 12 | 288 | 13 | 2 | 273 |
| PPP 177 | 2.1 | 125.0 | 6 | 2 | 0 | 4 | 15 | 2 | 0 | 13 |
| PPP 178 | 2.1 | 125.0 | 14 | 5 | 2 | 7 | 77 | 5 | 2 | 70 |
| PPP 214 | 2.0 | | 10 | 4 | 2 | 4 | 136 | 4 | 2 | 130 |
| Limon Basin | | | | | | | | | | |
| PPP 679 | 3.5 | 30.0 | 16 | 2 | 8 | 6 | 475 | 20 | 134 | 321 |
| PPP 683 | 3.5 | 30.0 | 7 | 1 | 2 | 4 | 124 | 1 | 2 | 121 |
| PPP 695 | 3.5 | 30.0 | 6 | 1 | 0 | 5 | 33 | 1 | 0 | 32 |
| PPP 704 | 3.5 | | 30 | 16 | 7 | 7 | 201 | 34 | 34 | 133 |
| PPP 705 | 3.5 | | 13 | 5 | 3 | 5 | 49 | 5 | 3 | 41 |
| PPP 708 | 3.5 | | 25 | 6 | 11 | 8 | 484 | 15 | 119 | 350 |
| PPP 709 | 3.5 | 30.0 | 53 | 31 | 13 | 9 | 1196 | 202 | 364 | 630 |
| PPP 720 | 3.5 | 30.0 | 48 | 20 | 18 | 10 | 696 | 56 | 279 | 361 |
| PPP 722 | 3.5 | 30.0 | 44 | 19 | 15 | 10 | 1079 | 172 | 465 | 442 |
| PPP 723 | 3.5 | 30.0 | 42 | 19 | 13 | 10 | 1347 | 172 | 454 | 721 |
| PPP 932 | 3.5 | 12.5 | 14 | 2 | 6 | 6 | 239 | 2 | 24 | 213 |
| PPP 933 | 3.5 | 12.5 | 10 | 3 | 2 | 5 | 226 | 3 | 2 | 221 |
| PPP 935 | 3.5 | 12.5 | 6 | 0 | 2 | 4 | 42 | 0 | 11 | 31 |
| PPP 937 | 3.5 | 12.5 | 17 | 8 | 3 | 6 | 179 | 26 | 3 | 150 |
| PPP 939 | 3.5 | | 9 | 1 | 3 | 5 | 126 | 1 | 3 | 122 |
| PPP 940 | 3.5 | | 8 | 0 | 3 | 5 | 26 | 0 | 3 | 23 |
| PPP 697 | 3.3 | 30.0 | 11 | 2 | 3 | 6 | 164 | 2 | 12 | 150 |
| PPP 663 | 3.1 | 5.0 | 27 | 12 | 12 | 3 | 378 | 21 | 345 | 12 |
| PPP 668 | 3.1 | 30.0 | 11 | 3 | 1 | 7 | 146 | 3 | 1 | 142 |
| PPP 669 | 3.1 | 30.0 | 8 | 2 | 0 | 6 | 44 | 2 | 0 | 42 |
| PPP 670 | 3.1 | 30.0 | 18 | 10 | 1 | 7 | 243 | 10 | 1 | 232 |
| PPP 671 | 3.1 | 30.0 | 8 | 4 | 1 | 3 | 17 | 4 | 1 | 12 |
| PPP 672 | 3.1 | 30.0 | 7 | 3 | 1 | 3 | 25 | 3 | 1 | 21 |
| PPP 689 | 3.1 | 30.0 | 7 | 0 | 2 | 5 | 43 | 0 | 2 | 41 |
| PPP 691 | 3.1 | 30.0 | 9 | 1 | 2 | 6 | 234 | 1 | 2 | 231 |
| PPP 180 | 2.8 | 125.0 | 21 | 8 | 6 | 7 | 183 | 35 | 6 | 142 |
| PPP 634 | 1.7 | 61.5 | 45 | 31 | 9 | 5 | 378 | 94 | 153 | 131 |
| PPP 635 | 1.7 | 61.5 | 41 | 24 | 9 | 8 | 860 | 186 | 234 | 440 |
| PPP 639 | 1.7 | 61.5 | 49 | 37 | 4 | 8 | 283 | 190 | 13 | 80 |
| PPP 640 | 1.7 | 61.5 | 44 | 29 | 8 | 7 | 1052 | 29 | 233 | 610 |
| PPP 642 | 1.7 | 61.5 | 39 | 26 | 8 | 5 | 561 | 323 | 233 | 5 |
| PPP 644 | 1.7 | 61.5 | 26 | 15 | 6 | 5 | 44 | 24 | 15 | 5 |
| PPP 645 | 1.7 | 61.5 | 30 | 20 | 7 | 3 | 102 | 47 | 52 | 3 |
| PPP 710 | 1.7 | 61.5 | 31 | 20 | 6 | 5 | 94 | 56 | 6 | 32 |
| PPP 653 | 1.6 | 200.0 | 25 | 13 | 8 | 4 | 97 | 31 | 35 | 31 |
| PPP 738 | 1.6 | | 29 | 18 | 8 | 3 | 164 | 27 | 125 | 12 |
| PPP 943 | 1.6 | 61.5 | 35 | 21 | 10 | 4 | 224 | 66 | 136 | 22 |

Table 1.—Continued.

| Collection number | Age (Ma) | Paleodepth (m) | Number of species |  |  |  | Abundance |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  | Total | Encrusting | Erect | Free-living | Total | Encrusting | Erect | Free-living |
| PPP 944 | 1.6 | 61.5 | 52 | 33 | 12 | 7 | 1645 | 1059 | 246 | 340 |
| PPP 948 | 1.6 | 61.5 | 38 | 20 | 11 | 7 | 497 | 191 | 254 | 52 |
| PPP 949 | 1.6 | 61.5 | 59 | 45 | 10 | 4 | 608 | 171 | 433 | 4 |
| PPP 950 | 1.6 | 61.5 | 58 | 42 | 10 | 6 | 958 | 546 | 361 | 51 |
| PPP 962 | 1.6 | 61.5 | 52 | 33 | 13 | 6 | 484 | 159 | 274 | 51 |
| PPP 963 | 1.6 | 61.5 | 56 | 40 | 11 | 5 | 551 | 283 | 245 | 23 |
| PPP 631 | 1.6 | 75.0 | 48 | 28 | 11 | 9 | 1578 | 514 | 254 | 810 |
| PPP 712 | 1.6 | 20.0 | 20 | 11 | 5 | 4 | 200 | 56 | 113 | 31 |
| Burica region |  |  |  |  |  |  |  |  |  |  |
| PPP 47 | 1.8 |  | 32 | 30 | 0 | 2 | 50 | 30 | 0 | 20 |
| PPP 86 | 1.8 |  | 55 | 49 | 4 | 2 | 253 | 220 | 22 | 11 |
| PPP 137 | 1.8 |  | 17 | 14 | 1 | 2 | 17 | 14 | 1 | 2 |
| PPP 144 | 1.8 |  | 47 | 40 | 4 | 3 | 128 | 103 | 22 | 3 |
| PPP 146 | 1.8 |  | 40 | 35 | 2 | 3 | 85 | 53 | 11 | 21 |
| PPP 148 | 1.8 |  | 37 | 35 | 0 | 2 | 82 | 71 | 0 | 11 |
| PPP 156 | 1.8 |  | 34 | 29 | 3 | 2 | 43 | 38 | 3 | 2 |
| Nicoya Peninsula |  |  |  |  |  |  |  |  |  |  |
| PPP 832 | 1.0 |  | 10 | 6 | 1 | 3 | 37 | 6 | 10 | 21 |
| PPP 833 | 1.0 |  | 7 | 3 | 1 | 3 | 25 | 12 | 1 | 12 |

1990; Coates *et al.*, 1992; Coates and Obando, 1996). Equally importantly, the abundant, often well preserved cheilostome material has provided a new resource for applying finer-scale, quantitative morphologic approaches to taxonomic distinctions (Jackson and Cheetham, 1990, 1994).

Previous work on cheilostomes from the PPP and DR collections has focused on evolutionary patterns in two genera, *Metrarabdotos* and *Stylopoma* (Cheetham, 1986, 1987; Cheetham and Hayek, 1988; Jackson and Cheetham, 1994; Cheetham *et al.*, 1994; Cheetham and Jackson, 1995, 1996). Here we consider the fauna as a whole, even though a sizable proportion of the species remains undescribed. The need for additional taxonomic splitting will no doubt become apparent as the fauna is studied in more detail. This paper is thus a general survey, the purpose of which is to provide initial estimates of: (1) the diversity of the PPP and DR cheilostomes and their affinities with the living and fossil fauna of the Caribbean; (2) the adequacy with which the PPP and DR collections reflect the diversity and affinities of this fauna; and (3) the spatial and temporal distribution of species, their abundance, and their colony growth forms within and across areas.

Preliminary study of 204 PPP collections (each of which was obtained from a roughly 10-kg sediment sample) has yielded 179 cheilostome taxa identified to species, 70 (39%) of which remain undescribed. Unlike other studies in this volume, ours incorporates 26 PPP collections from the Pacific side of the isthmus (with a total of 73 species), in addition to 124 DR collections (with a total of 132 cheilostome species). An even greater proportion of the DR species is undescribed (59%). Inclusion of these other collections allows us to estimate the minimum diversity of the Neogene tropical American cheilostome fauna at 250 species (53% of which are undescribed), just slightly under the 273 species estimated to be present in the living cheilostome fauna of the tropical western Atlantic (Schopf, 1973). The number of species is likely to grow significantly as both the PPP and DR collections are studied in more detail, and as new PPP collections from both sides of the isthmus are included. However, the same is probably true for the living Caribbean fauna. Recent studies have shown that correspondence between morphologic and genetic differences is maximized by splitting morphospecies to the limits of statistical significance; thus, many widely distributed, morphologically variable "species" probably represent suites of genetically distinct species (Jackson and Cheetham, 1990, 1994). We have attempted to use these findings as a guideline for the initial analysis of the PPP and DR collections by recognizing even the smallest observed morphologic differences as tentative species distinctions, pending more detailed (morphometric and statistical) study.

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## DISTRIBUTION, AGE, AND ADEQUACY OF COLLECTIONS

The 204 PPP collections represent five of the major Panamanian-Costa Rican regions listed in the PPP Database (Kaufmann, this volume) and shown on maps of the PPP collection sites (Appendix A): (1) Bocas del Toro Basin (Bocas del Toro Province, Caribbean Panama), 87 collections; (2) Canal Basin (Caribbean Panama), 10 collections; (3) Limon Basin (Caribbean Costa Rica), 66 collections; (4) Darien (Darien Province, Pacific Panama), 15 collections; and (5) the Pacific coasts of Panama and Costa Rica (Burica, Osa, Nicoya, and Golfo Dulce), 26 collections. Each bryozoan collection comprises specimens picked from a bulk sample (approximately 10 kg) of unconsolidated sediment. A collection contains 1–59 species (median 8; mean 14.4; CV [coefficient of variation] 103%). Sixty-two percent (126) of the 204 collections comprise 6 or more species each; the median number of species in these collections increases to 17 (mean 21.8) and CV decreases to 67%. These collections are from all the major regions except the Darien (Table 1).

The DR collections comprise 124 bulk samples, each consisting of 2 to more than 20 liters of sediment, and 63 sets of individually collected specimens (Saunders *et al.*, 1986). The collections from bulk samples include 1–40 species each (median 19, mean 17.7, CV 50%); the individually collected sets include a median number of 2 species (mean 3.2, CV 96%). Species from the non-bulk collections were combined with those from stratigraphically equivalent bulk samples in the same section; there was virtually no change in the median or mean number of species, or in the CV (18, 17.6, and 49%, respectively) from those of the bulk collections. The DR collections represent four of the nine major areas in the Cibao region of the northern Dominican Republic (Saunders *et al.*, 1986, text-fig. 3): Rio Cana, 22 collections; Rio Gurabo, 61 collections; Rio Mao, 21 collections; and Rio Yaque del Norte, 20 collections. A total of 117 collections (94%) include 6 species or more; these collections represent all four areas (Table 2). The average number of species in these collections (median 19, mean 18.5) is about the same as that for the 124 PPP collections with 6 or more species (median 17, mean 21.8), but is less variable (CV 44% compared to 67%) and has a smaller maximum (41 species compared to 59).

The greater variability in apparent diversity (*i.e.*, the number of species recovered) of the PPP collections is probably at least partly a function of preservation. Many collections were made from units that are not obviously fossiliferous, and the quality of bryozoan specimens is correspondingly variable. However, the most abundant and ubiquitous bryozoans in the PPP, even in the collections with the lowest diversity, are species with generally less preservable aragonitic skeletons. Thus, the numbers of species likely vary with other (*e.g.*, environmental) factors as well.

The temporal distribution of PPP and DR bryozoan collections and their abundance is shown in Text-figure 2, together with the distribution of numbers of species represented in each area and occurring in both. Abundance totals more than 39,000 for the PPP and more than 21,000 for the DR, but these are minimum values based on counts of colonies and colony fragments converted to a scale coded as follows: 1–9 = 1 (rare), 10–99 = 10 (common), and 100+ = 100 (abundant). For each of the DR collections, counting was stopped at 100 for any given species, whereas actual counts were recorded in the PPP Database. Basing calculations on the coded scale reduces over-dominance by the most abundant species (especially in the PPP collections) and helps increase comparability of the PPP and DR data.

Taken together, the PPP and DR collections span an interval from late Early or early Middle Miocene (calcareous nannoplankton zones NN 4–6, approximately 17–13 Ma) to Pleistocene (zone NN 19, approximately 0.5–2 Ma), with the two sets of collections overlapping in age by about 8 m.y., or half the approximately 16-m.y. interval (Text-fig. 2). However, the PPP collections (median age 3.5 Ma, range 11.6–1 Ma) are generally younger than those from the DR (median age 7.1 Ma, range 17–3 Ma); 84% of the PPP collections are concentrated in the interval younger than 5 Ma, whereas 87% of those from the DR are older than 5 Ma. The contrast is even more pronounced in terms of abundance, with 98% of PPP abundance concentrated in the younger interval and 93% of DR abundance from the older. The 8–7 Ma (Late Miocene, exclusively DR) and 4–3 Ma (Early Pliocene, chiefly PPP) intervals are especially well sampled. The paucity of collections in both areas in the long interval between 15 and 8 Ma (Middle and early Late Miocene) stands in marked contrast.

The situation with respect to the number of species recovered is less uneven (Text-fig. 2C). Of the 179

Table 2.—Diversity and abundance of cheilostome bryozoans (total and by growth form) in Dominican Republic project (DR) collections containing six or more species each.

| Collection number | Age (Ma) | Number of species | | | | Abundance | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Total | Encrusting | Erect | Free-living | Total | Encrusting | Erect | Free-living |
| Rio Yaque del Norte | | | | | | | | | |
| NMB 17283 | 16.2 | 11 | 2 | 6 | 3 | 119 | 2 | 6 | 111 |
| NMB 17285 | 16.1 | 9 | 1 | 6 | 2 | 54 | 1 | 33 | 20 |
| NMB 17286 | 16.0 | 12 | 2 | 7 | 3 | 255 | 11 | 43 | 201 |
| NMB 17287 | 15.9 | 11 | 1 | 7 | 3 | 164 | 1 | 52 | 111 |
| NMB 17288 | 15.8 | 14 | 3 | 8 | 3 | 356 | 3 | 143 | 210 |
| NMB 17289 | 15.8 | 12 | 2 | 7 | 3 | 147 | 2 | 25 | 120 |
| NMB 17290 | 15.7 | 12 | 2 | 7 | 3 | 174 | 20 | 34 | 120 |
| NMB 17327 | 15.7 | 13 | 2 | 8 | 3 | 247 | 2 | 224 | 21 |
| NMB 17184 | 15.7 | 25 | 4 | 18 | 3 | 493 | 13 | 369 | 111 |
| NMB 16935 | 15.6 | 27 | 7 | 17 | 3 | 288 | 16 | 161 | 111 |
| Olsson 179 | 15.5 | 32 | 10 | 19 | 3 | 383 | 19 | 253 | 111 |
| NMB 17265 | 15.5 | 19 | 6 | 11 | 2 | 82 | 15 | 56 | 11 |
| NMB 16936 | 15.5 | 18 | 6 | 10 | 2 | 459 | 105 | 244 | 110 |
| NMB 16938 | 15.4 | 20 | 6 | 11 | 3 | 290 | 15 | 164 | 111 |
| NMB 17190 | 15.4 | 14 | 2 | 10 | 2 | 41 | 2 | 28 | 11 |
| NMB 16942 | 15.4 | 18 | 5 | 11 | 2 | 261 | 23 | 137 | 101 |
| NMB 17278 | 5.6 | 6 | 2 | 4 | 0 | 6 | 2 | 4 | 0 |
| NMB 17268 | 4.6 | 25 | 9 | 13 | 3 | 70 | 9 | 31 | 30 |
| USGS 8702 | 3.9 | 31 | 10 | 17 | 4 | 139 | 10 | 98 | 31 |
| Rio Mao | | | | | | | | | |
| USGS 8525 | 8.0 | 27 | 10 | 13 | 4 | 378 | 19 | 346 | 13 |
| NMB 17269 | 8.0 | 22 | 9 | 10 | 3 | 121 | 63 | 37 | 21 |
| NMB 16913 | 8.0 | 22 | 9 | 10 | 3 | 202 | 27 | 154 | 21 |
| NMB 16912 | 7.9 | 6 | 1 | 2 | 3 | 33 | 1 | 11 | 21 |
| NMB 16922 | 7.9 | 15 | 7 | 5 | 3 | 204 | 52 | 32 | 120 |
| NMB 16927 | 7.8 | 22 | 9 | 10 | 3 | 292 | 36 | 226 | 30 |
| NMB 16923 | 7.8 | 10 | 4 | 3 | 3 | 55 | 13 | 21 | 21 |
| NMB 16917 | 7.8 | 14 | 7 | 4 | 3 | 149 | 16 | 22 | 111 |
| NMB 16916 | 7.8 | 27 | 13 | 12 | 2 | 360 | 94 | 246 | 20 |
| NMB 16915 | 7.8 | 18 | 8 | 7 | 3 | 279 | 26 | 43 | 210 |
| NMB 16926 | 7.8 | 22 | 9 | 10 | 3 | 103 | 27 | 46 | 30 |
| NMB 16924 | 7.8 | 18 | 6 | 9 | 3 | 387 | 24 | 243 | 120 |
| NMB 16918 | 7.8 | 21 | 7 | 11 | 3 | 489 | 43 | 236 | 210 |
| NMB 16928 | 7.7 | 26 | 15 | 9 | 2 | 656 | 114 | 432 | 110 |
| NMB 16929 | 7.6 | 25 | 11 | 11 | 3 | 430 | 155 | 254 | 21 |
| NMB 16932 | 7.6 | 10 | 4 | 3 | 3 | 55 | 4 | 21 | 30 |
| NMB 16914 | 7.6 | 13 | 7 | 3 | 3 | 85 | 25 | 30 | 30 |
| NMB 16930 | 7.5 | 12 | 3 | 6 | 3 | 147 | 3 | 114 | 30 |
| NMB 16802 | 7.5 | 9 | 3 | 3 | 3 | 144 | 3 | 21 | 120 |
| NMB 16910 | 7.4 | 22 | 5 | 13 | 4 | 211 | 23 | 67 | 121 |
| NMB 17175 | 7.4 | 21 | 6 | 10 | 5 | 102 | 24 | 46 | 32 |
| Rio Gurabo | | | | | | | | | |
| NMB 15915 | 7.9 | 20 | 10 | 7 | 3 | 173 | 28 | 115 | 30 |
| NMB 15914 | 7.9 | 18 | 10 | 5 | 3 | 243 | 19 | 104 | 120 |
| NMB 15912 | 7.9 | 20 | 9 | 8 | 3 | 164 | 18 | 125 | 21 |
| NMB 15911 | 7.8 | 21 | 10 | 8 | 3 | 174 | 19 | 125 | 30 |
| NMB 15910 | 7.8 | 11 | 2 | 6 | 3 | 47 | 20 | 6 | 21 |
| NMB 15903 | 7.8 | 10 | 3 | 4 | 3 | 28 | 3 | 4 | 21 |
| NMB 16192 | 7.7 | 10 | 5 | 2 | 3 | 28 | 5 | 2 | 21 |
| NMB 15900 | 7.7 | 20 | 6 | 11 | 3 | 83 | 15 | 38 | 30 |
| NMB 15901 | 7.7 | 13 | 3 | 7 | 3 | 58 | 3 | 34 | 21 |
| NMB 16191 | 7.7 | 6 | 1 | 2 | 3 | 15 | 1 | 2 | 12 |
| NMB 15904 | 7.7 | 9 | 2 | 4 | 3 | 36 | 11 | 4 | 21 |
| NMB 15907 | 7.7 | 9 | 2 | 4 | 3 | 45 | 11 | 13 | 21 |
| NMB 15906 | 7.6 | 15 | 4 | 8 | 3 | 294 | 22 | 62 | 210 |

Table 2.—Continued.

| Collection number | Age (Ma) | Number of species | | | | Abundance | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Total | Encrusting | Erect | Free-living | Total | Encrusting | Erect | Free-living |
| NMB 15897 | 7.6 | 6 | 2 | 1 | 3 | 123 | 2 | 1 | 120 |
| NMB 15896 | 7.6 | 6 | 1 | 2 | 3 | 303 | 1 | 2 | 300 |
| NMB 16186 | 7.5 | 9 | 2 | 4 | 3 | 45 | 2 | 13 | 30 |
| NMB 15890 | 7.3 | 10 | 3 | 4 | 3 | 235 | 3 | 112 | 120 |
| NMB 15882 | 7.2 | 20 | 9 | 8 | 3 | 380 | 36 | 323 | 21 |
| NMB 15881 | 7.2 | 19 | 7 | 9 | 3 | 262 | 16 | 234 | 12 |
| NMB 16167 | 7.2 | 19 | 7 | 9 | 3 | 82 | 16 | 54 | 12 |
| NMB 15878 | 7.2 | 23 | 10 | 10 | 3 | 500 | 55 | 325 | 120 |
| NMB 15876 | 7.1 | 8 | 3 | 2 | 3 | 17 | 3 | 11 | 3 |
| NMB 15874 | 7.0 | 7 | 1 | 2 | 4 | 34 | 1 | 2 | 31 |
| NMB 15873 | 7.0 | 7 | 1 | 3 | 3 | 133 | 1 | 12 | 120 |
| NMB 16810 | 7.0 | 9 | 1 | 4 | 4 | 45 | 1 | 13 | 31 |
| NMB 15865 | 7.0 | 16 | 5 | 7 | 4 | 160 | 14 | 124 | 22 |
| NMB 15871 | 7.0 | 11 | 3 | 5 | 3 | 245 | 111 | 23 | 111 |
| NMB 15869 | 6.9 | 12 | 4 | 4 | 4 | 156 | 22 | 13 | 121 |
| NMB 15864 | 6.9 | 15 | 3 | 8 | 4 | 249 | 3 | 26 | 220 |
| NMB 15863 | 6.8 | 21 | 5 | 12 | 4 | 291 | 5 | 165 | 121 |
| NMB 15860 | 6.7 | 27 | 7 | 16 | 4 | 243 | 25 | 196 | 22 |
| NMB 15849 | 6.6 | 33 | 18 | 14 | 1 | 258 | 90 | 158 | 10 |
| NMB 16811 | 6.5 | 21 | 15 | 6 | 0 | 75 | 51 | 24 | 0 |
| NMB 15854 | 6.5 | 15 | 8 | 6 | 1 | 69 | 35 | 24 | 10 |
| NMB 15851 | 6.5 | 22 | 17 | 5 | 0 | 175 | 53 | 122 | 0 |
| NMB 15853 | 6.5 | 24 | 18 | 6 | 0 | 222 | 81 | 141 | 0 |
| NMB 15846 | 6.5 | 29 | 13 | 14 | 2 | 254 | 67 | 176 | 11 |
| NMB 15842 | 6.2 | 26 | 10 | 14 | 2 | 116 | 28 | 77 | 11 |
| NMB 15840 | 5.8 | 11 | 5 | 4 | 2 | 29 | 5 | 13 | 11 |
| NMB 15837 | 5.8 | 16 | 5 | 11 | 0 | 52 | 14 | 38 | 0 |
| NMB 15838 | 5.7 | 26 | 13 | 10 | 3 | 71 | 22 | 46 | 3 |
| NMB 15836 | 5.7 | 15 | 5 | 5 | 5 | 78 | 5 | 32 | 41 |
| NMB 15835 | 5.6 | 21 | 5 | 10 | 6 | 201 | 23 | 46 | 132 |
| NMB 15805 | 5.5 | 17 | 4 | 8 | 5 | 152 | 13 | 8 | 131 |
| NMB 15962 | 5.4 | 31 | 11 | 15 | 5 | 319 | 38 | 231 | 50 |
| NMB 15804 | 5.4 | 21 | 5 | 12 | 4 | 66 | 5 | 30 | 31 |
| NMB 15934 | 5.4 | 27 | 8 | 14 | 5 | 126 | 17 | 77 | 32 |
| NMB 15815 | 5.3 | 26 | 9 | 12 | 5 | 206 | 18 | 57 | 131 |
| NMB 15964 | 5.3 | 19 | 5 | 9 | 5 | 64 | 5 | 27 | 32 |
| NMB 15814 | 5.3 | 24 | 7 | 12 | 5 | 87 | 7 | 39 | 41 |
| NMB 15823 | 3.9 | 20 | 4 | 14 | 2 | 74 | 4 | 68 | 2 |
| NMB 15828 | 3.8 | 10 | 3 | 7 | 0 | 37 | 3 | 34 | 0 |
| NMB 16103 | 3.7 | 6 | 3 | 2 | 1 | 6 | 3 | 2 | 1 |
| NMB 15829 | 3.7 | 11 | 7 | 2 | 2 | 11 | 7 | 2 | 2 |
| NMB 15832 | 3.4 | 8 | 3 | 5 | 0 | 134 | 3 | 131 | 0 |
| NMB 15833 | 3.4 | 12 | 4 | 5 | 3 | 66 | 31 | 23 | 12 |
| Rio Cana | | | | | | | | | |
| NMB 16857 | 7.3 | 21 | 11 | 7 | 3 | 372 | 29 | 133 | 210 |
| NMB 16856 | 7.1 | 31 | 19 | 8 | 4 | 85 | 37 | 26 | 22 |
| NMB 16855 | 7.1 | 14 | 12 | 1 | 1 | 32 | 21 | 1 | 10 |
| NMB 16995 | 6.5 | 19 | 9 | 8 | 2 | 163 | 36 | 125 | 2 |
| NMB 16844 | 6.5 | 20 | 7 | 11 | 2 | 128 | 52 | 74 | 2 |
| NMB 16842 | 6.5 | 26 | 12 | 11 | 3 | 98 | 30 | 47 | 21 |
| NMB 16841 | 6.5 | 6 | 2 | 4 | 0 | 6 | 2 | 4 | 0 |
| NMB 16839 | 6.5 | 21 | 12 | 7 | 2 | 219 | 57 | 160 | 2 |
| NMB 16838 | 6.5 | 29 | 15 | 11 | 3 | 245 | 69 | 155 | 21 |
| NMB 16837 | 6.4 | 22 | 13 | 6 | 3 | 193 | 139 | 33 | 21 |
| NMB 16836 | 6.4 | 31 | 19 | 10 | 2 | 742 | 406 | 334 | 2 |
| NMB 16835 | 6.3 | 26 | 13 | 11 | 2 | 197 | 31 | 155 | 11 |
| NMB 16834 | 6.0 | 25 | 14 | 9 | 2 | 133 | 59 | 72 | 2 |

Table 2.—Continued.

| Collection number | Age (Ma) | Number of species: Total | Encrusting | Erect | Free-living | Abundance: Total | Encrusting | Erect | Free-living |
|---|---|---|---|---|---|---|---|---|---|
| NMB 16833 | 5.9 | 39 | 20 | 17 | 2 | 237 | 92 | 125 | 20 |
| NMB 16832 | 5.9 | 31 | 17 | 12 | 2 | 148 | 71 | 66 | 11 |
| NMB 16828 | 5.7 | 37 | 16 | 17 | 4 | 397 | 79 | 296 | 22 |
| NMB 16818 | 5.0 | 37 | 18 | 16 | 3 | 271 | 54 | 187 | 30 |
| NMB 16817 | 5.0 | 37 | 15 | 19 | 3 | 307 | 78 | 208 | 21 |
| NMB 16860 | 4.5 | 8 | 3 | 2 | 3 | 17 | 12 | 2 | 3 |
| NMB 16865 | 3.8 | 22 | 15 | 3 | 4 | 49 | 33 | 3 | 13 |
| NMB 17023 | 3.1 | 32 | 14 | 16 | 2 | 284 | 14 | 268 | 2 |

species that occur in the PPP, 134 (75%) are found in the 4–3 Ma (Early Pliocene) interval, which also contains 78 (59%) of the 132 species that occur in the DR. The numbers of species in other 1-m.y. intervals, except that between 5 and 4 Ma, are more biased toward one area or the other (Text-fig. 2C). However, the cumulative fauna in the 3-m.y. interval from the latest Miocene to mid-Pliocene (6–3 Ma) includes fully 72% (85) of the 118 species found only in the PPP, 66% (47) of the 71 present only in the DR, and 97% (59) of the 61 occurring in both areas. By this criterion, the 6–3 Ma at least appears well sampled.

For a more detailed estimate of sampling adequacy (*i.e.*, the probability that the numbers of species recovered represent a major proportion of those present), we plotted cumulative numbers of species recovered as a function of the numbers of collections examined in each area (Text-fig. 3). In both plots, collections were added region by region (PPP) or section by section (DR), from oldest to youngest within each region or section. Although the DR has fewer species and collections than the PPP, the overall rate of increase in species is the same in the two plots, and the curves are similar in shape, rising in a series of steps corresponding to the different areas sampled. Overall, a slight flattening of the curves is apparent (thus indicating at least the beginning of an approach to "true" diversity): distinctly more than 50% of the species were recovered after 50% of the collections were tallied (124 species, or 69%, in the PPP, and 93 species, or 70% in the DR). Flattening is somewhat more apparent in the DR curve, with recovery of 50% of the total number of species requiring only 16% of the collections, compared with 30% for the PPP.

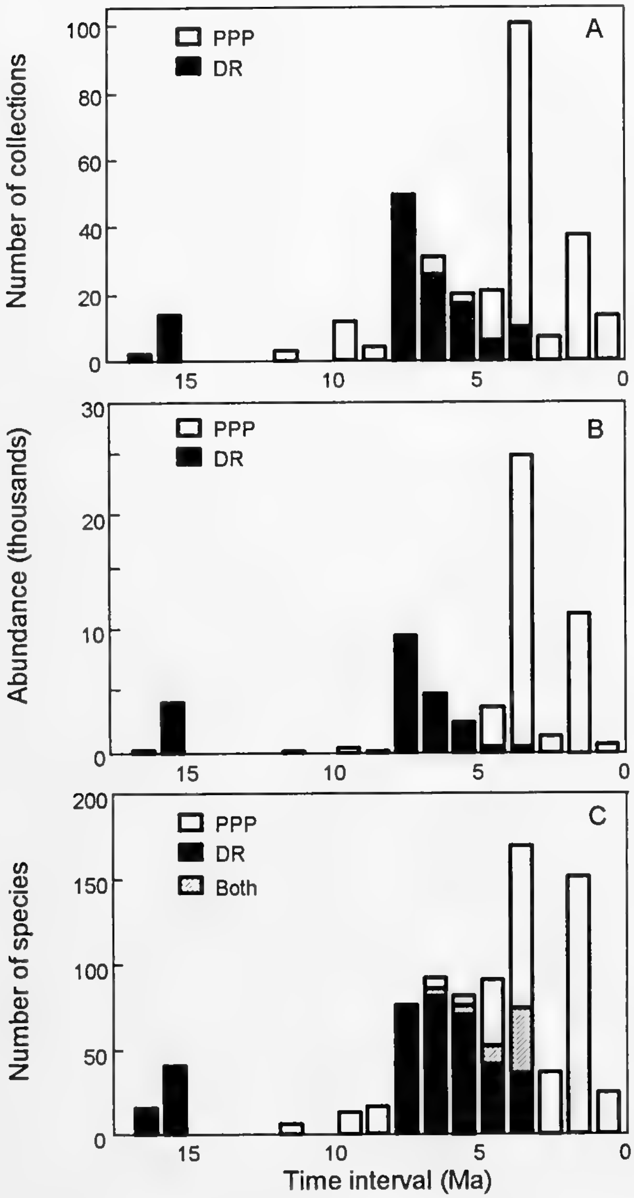
If sampling is somewhat better for the DR than the PPP, as suggested by the collecting curves in Text-figure 3, PPP diversity can ultimately be expected to exceed that for the DR by even more than the 36% reflected in the total numbers of species so far recovered. This may well be related to the greater size and heterogeneity of the area sampled by the PPP (Text-fig. 1); the DR collections are all from a single sedimentary basin, the Cibao Basin of the northern Dominican Republic, little more than 100 km across (Saunders *et al.*, 1986, text-fig. 2), whereas the area sampled for the PPP is nearly 1000 km long. However, comparison of curves for individual well-sampled PPP and DR areas (Text-fig. 4) suggests that PPP diversity consistently exceeds that for the DR even on scales of tens of km. The same is true for time intervals (Text-fig. 4). Moreover, similar plots of diversity against cumulative abundance (not shown) have virtually the same form as those plotted against numbers of collections. Thus, the differences in total numbers of cheilostome species appear to reflect real differences in "true" diversity.

Even though some of the PPP collections contain up to 44% more species and more than twice the abundance of the richest DR collections, the proportion of PPP collections characterized by few species and low abundance is much greater than that in the DR (Text-fig. 5). As noted above, 38% of PPP collections but only 6% of those from the DR include fewer than six species each. Indeed, the modal number of species per DR collection slightly exceeds the median number (20 *versus* 19), whereas the modal number in the PPP is just one species (Text-fig. 5) compared to a median of 8. The preponderance of low diversity collections in the PPP, together with the higher total number of species, illustrates why the estimation of "true" diversity is even less certain than for the DR.

## ABUNDANCE AND DISTRIBUTION OF SPECIES AND GROWTH FORMS

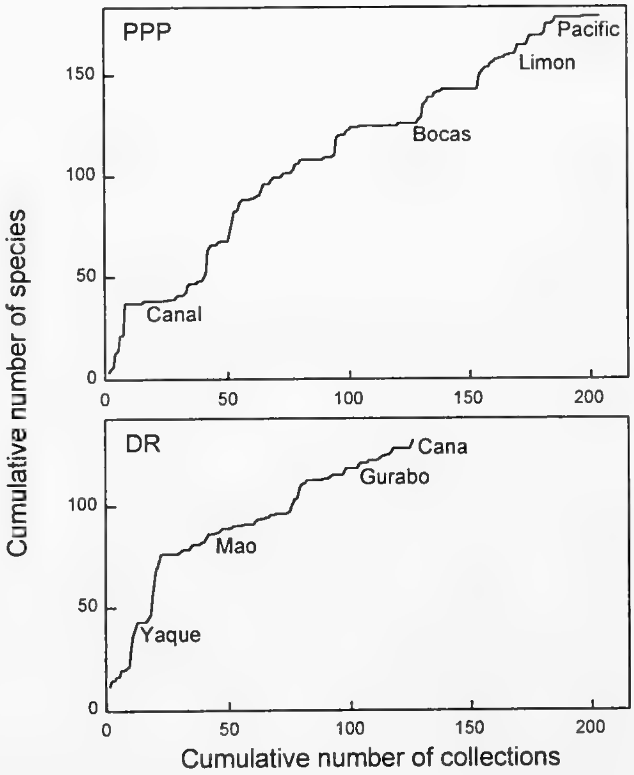
### GROWTH FORMS AND THE ADEQUACY OF COLLECTIONS

Species were assigned to three major colony growth-form categories (Table 3): encrusting (EN), erect (EF, erect flexible; ER, erect rigid), and free-living (FL). Examples of PPP and DR species with these growth forms are illustrated in Cheetham and Jackson (1999). We used this generalized approach, rather than

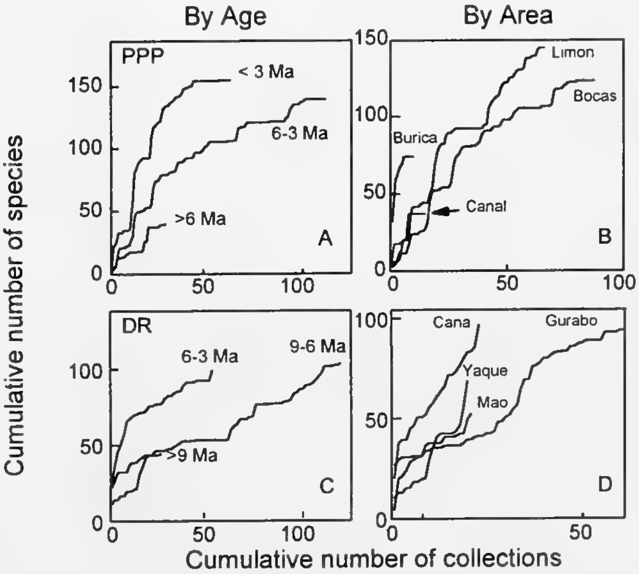


Text-figure 2.—Temporal distribution of 204 PPP and 124 DR collections, the abundance of bryozoan specimens (total 60,757; see text for counting method), and the numbers of species (total 250) represented in each interval. Ages of collections are medians of ranges; collections are grouped in 1-m.y. "bins" ending in whole units, *e.g.*, 3.1–4.0 Ma.

a more detailed classification such as that of Hageman *et al.* (1998), for two reasons. First, the great majority of species, 67%, show relatively little variation in possessing single- to multilayered sheetlike or platelike colonies. With few exceptions, species in the encrusting category occur as small, usually rare colony fragments. Thus, the scope for recognizing subsets of morphologies in this group is restricted. Secondly, although erect and free-living species show many, much



Text-figure 3.—Cumulative curves (collecting curves) of species recovered with increasing numbers of collections examined (total 204 for PPP, 124 for DR). For each area, collections were added region by region (PPP) or section by section (DR), from oldest to youngest in each.



Text-figure 4.—Cumulative collecting curves for PPP and DR collections, each grouped by 3-m.y. interval and by region or section.

Table 3.—Growth forms, abundances, and numbers of PPP and DR collections in which each occurs (= occurrences) of the 71 most common cheilostome bryozoan species (cumulative abundance > 100) arranged by rank in total abundance.

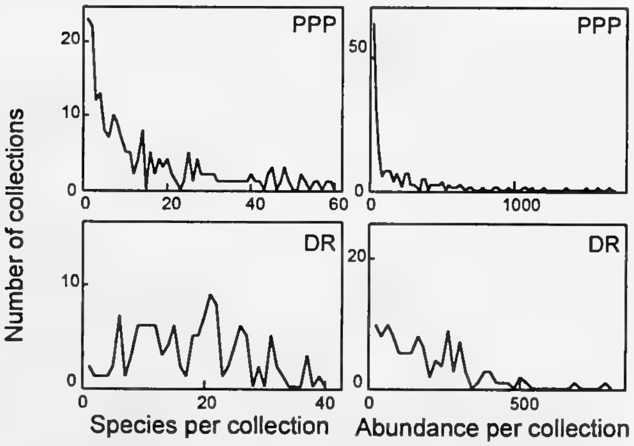
| Species | Growth form | Rank in abundance | Abundance in PPP | Abundance in DR | Rank in occurrences | Occurrences in PPP | Occurrences in DR |
|---|---|---|---|---|---|---|---|
| *Cupuladria biporosa* | FL | 1 | 4410 | 2543 | 1 | 133 | 113 |
| *Discoporella* n. sp. 6 | FL | 2 | 4451 | 0 | 5 | 121 | 0 |
| *Mamillopora tuberosa* | FL | 3 | 2974 | 861 | 2 | 112 | 96 |
| *Cupuladria* n. sp. 1 aff. *C. biporosa* | FL | 4 | 2742 | 0 | 14 | 77 | 0 |
| *Cupuladria* n. sp. 4 aff. *C. canariensis* | FL | 5 | 2205 | 0 | 7 | 108 | 0 |
| *Nellia tenella* | EF | 6 | 870 | 1250 | 4 | 60 | 71 |
| *Discoporella* n. sp. 1 | FL | 7 | 0 | 1889 | 13 | 0 | 80 |
| *Thalmoporella biperforata* | ER | 8 | 8 | 1865 | 8 | 8 | 92 |
| *Tremogasterina mucronata* | EN | 9 | 1382 | 477 | 6 | 41 | 72 |
| *Discoporella* n. sp. 5 | FL | 10 | 1706 | 0 | 9 | 86 | 0 |
| *Reteporellina evelinae* | ER | 11 | 1550 | 125 | 30 | 38 | 8 |
| *Discoporella* n. sp. 7 | FL | 12 | 1436 | 0 | 9 | 86 | 0 |
| *Discoporella* n. sp. 4 | FL | 13 | 0 | 1340 | 84 | 0 | 17 |
| *Mamillopora cavernulosa* | FL | 14 | 1284 | 0 | 35 | 42 | 0 |
| *Metrarabdotos colligatum* | ER | 15 | 11 | 1153 | 39 | 2 | 37 |
| *Gemelliporella punctata* | ER | 16 | 389 | 720 | 15 | 29 | 45 |
| *Corynostylus labiatus* | EF | 17 | 13 | 989 | 39 | 4 | 35 |
| *Cellaria mandibulata* | EF | 18 | 824 | 65 | 34 | 23 | 20 |
| *Biflustra savartii* | EN | 19 | 602 | 281 | 3 | 89 | 74 |
| *Cupuladria* n. sp. 8 aff. *C. canariensis* | FL | 20 | 875 | 0 | 28 | 47 | 0 |
| *Discoporella* n. sp. 3 | FL | 21 | 828 | 13 | 38 | 36 | 4 |
| *Celleporaria albirostris* | EN | 22 | 834 | 0 | 47 | 33 | 0 |
| *Vibracellina laxibasis* | EN | 23 | 726 | 0 | 35 | 42 | 0 |
| *Semihaswellia sinuosa* | EF | 24 | 159 | 519 | 39 | 15 | 24 |
| *Metrarabdotos* n. sp. 10 | ER | 25 | 444 | 214 | 52 | 12 | 16 |
| *Schizoporella magniporosa* | ER | 26 | 55 | 535 | 18 | 10 | 58 |
| *Metrarabdotos auriculatum* | ER | 27 | 25 | 484 | 64 | 7 | 16 |
| *Schedocleidochasma* n. sp. 3 | EN | 28 | 501 | 0 | 23 | 51 | 0 |
| *Celleporaria brunnea* | EN | 29 | 310 | 160 | 19 | 49 | 16 |
| *Schedocleidochasma cleidostoma* | EN | 30 | 458 | 0 | 24 | 49 | 0 |
| *Scrupocellaria regularis* | EF | 31 | 446 | 0 | 37 | 41 | 0 |
| *Steginoporella parvicella* | EN | 32 | 26 | 398 | 16 | 8 | 65 |
| *Skylonia dohmi* | EF | 33 | 0 | 403 | 85 | 0 | 16 |
| *Scrupocellaria* n. sp. 1 | EF | 34 | 142 | 248 | 27 | 7 | 41 |
| *Mamillopora* n. sp. 1 | FL | 35 | 384 | 0 | 89 | 15 | 0 |
| *Bracebridgia subsulcata* | ER | 36 | 371 | 0 | 73 | 20 | 0 |
| *Buskea* n. sp. aff. *B. dichotoma* | ER | 37 | 365 | 0 | 92 | 14 | 0 |
| *Adeonellopsis* n. sp. 3 | ER | 38 | 355 | 0 | 101 | 13 | 0 |
| *Celleporaria magnifica* | EN | 39 | 54 | 258 | 17 | 18 | 51 |
| *Cupuladria* n. sp. 5 aff. *C. canariensis* | FL | 40 | 287 | 0 | 55 | 26 | 0 |
| *Stylopoma spongites* | EN | 41 | 110 | 176 | 46 | 11 | 23 |
| *Petraliella bisinuata* | EN | 42 | 283 | 0 | 67 | 22 | 0 |
| *Adeonellopsis deformis* | ER | 43 | 0 | 265 | 20 | 0 | 58 |
| *Margaretta buski* | EF | 44 | 261 | 0 | 45 | 36 | 0 |
| *Canda simplex* | EF | 45 | 190 | 57 | 24 | 28 | 21 |
| *Cigclisula porosa* | ER | 46 | 122 | 117 | 9 | 41 | 45 |
| *Labioporella miocenica* | EN | 47 | 0 | 238 | 24 | 0 | 49 |
| n. gen. B n. sp. y Scolaro | ER | 48 | 23 | 198 | 48 | 5 | 27 |
| *Hippoporella gorgonensis* | EN | 49 | 122 | 96 | 12 | 50 | 33 |
| *Ditaxipora* n. sp. 2 | EF | 50 | 0 | 202 | 173 | 0 | 4 |
| *Turbicellepora* n. sp. | EN | 51 | 201 | 0 | 39 | 39 | 0 |
| *Gemelliporella*? n. sp. | ER | 52 | 81 | 114 | 60 | 18 | 6 |
| *Steginoporella* n. sp. 1 | EN | 53 | 0 | 187 | 85 | 0 | 16 |
| *Margaretta* n. sp. 1 | EF | 54 | 0 | 172 | 21 | 0 | 55 |
| *Microporella umbracula* | EN | 54 | 172 | 0 | 52 | 28 | 0 |
| *Vincularia* n. sp. | EF | 56 | 0 | 158 | 92 | 0 | 14 |
| *Cellaria* aff. *C. bassleri* | EF | 57 | 43 | 111 | 118 | 7 | 3 |
| *Pasythea* n. sp. | EF | 58 | 0 | 149 | 64 | 0 | 23 |
| *Gemelliporidra multilamellosa* | EN | 59 | 147 | 0 | 69 | 21 | 0 |

Table 3.—Continued.

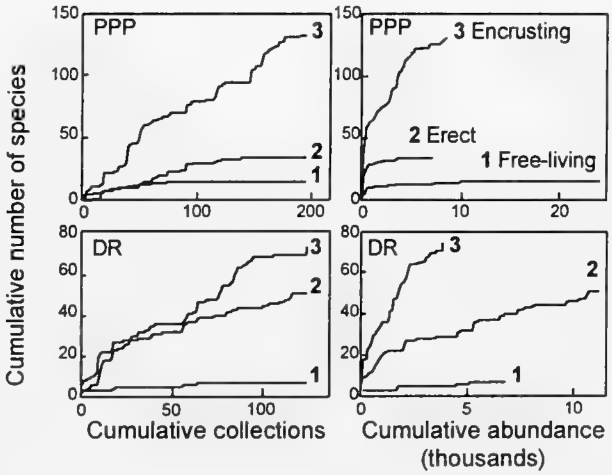
| Species | Growth form | Rank in abundance | Abundance in PPP | Abundance in DR | Rank in occurrences | Occurrences in PPP | Occurrences in DR |
|---|---|---|---|---|---|---|---|
| *Schedocleidochasma porcellanum* | EN | 60 | 4 | 141 | 30 | 4 | 42 |
| *Characodoma contractum* | EN | 61 | 134 | 0 | 22 | 53 | 0 |
| *Metrarabdotos lacrymosum* | ER | 61 | 11 | 123 | 33 | 2 | 42 |
| *Lagenicella* aff. *L. mexicana* | EN | 63 | 130 | 0 | 101 | 13 | 0 |
| *Parasmittina parsevaliformis* | EN | 64 | 70 | 49 | 44 | 25 | 13 |
| *Trematooecia vaughani* | EN | 65 | 0 | 113 | 64 | 0 | 23 |
| *Schizoporella cornuta* | EN | 66 | 110 | 0 | 28 | 47 | 0 |
| *Antropora leucocypha* | EN | 67 | 37 | 72 | 30 | 28 | 18 |
| *Hippaliosina rostrigera* | EN | 67 | 109 | 0 | 52 | 28 | 0 |
| *Metrarabdotos* n. sp. 4 | ER | 67 | 0 | 109 | 75 | 0 | 19 |
| *Stylopoma* n. sp. 11 | EN | 70 | 107 | 0 | 130 | 8 | 0 |
| *Steginoporella magnilabris* | EN | 71 | 99 | 2 | 50 | 27 | 2 |

more obvious differences in morphology, for example, in branch shapes and jointing (erect forms) or in permanent or intermittent nonattachment (free-living forms), they represent much smaller numbers of species which have similar patterns of occurrence and abundance (a possible exception is *Nellia tenella,* the only erect species occurring in more than 50 collections in both the PPP and DR).

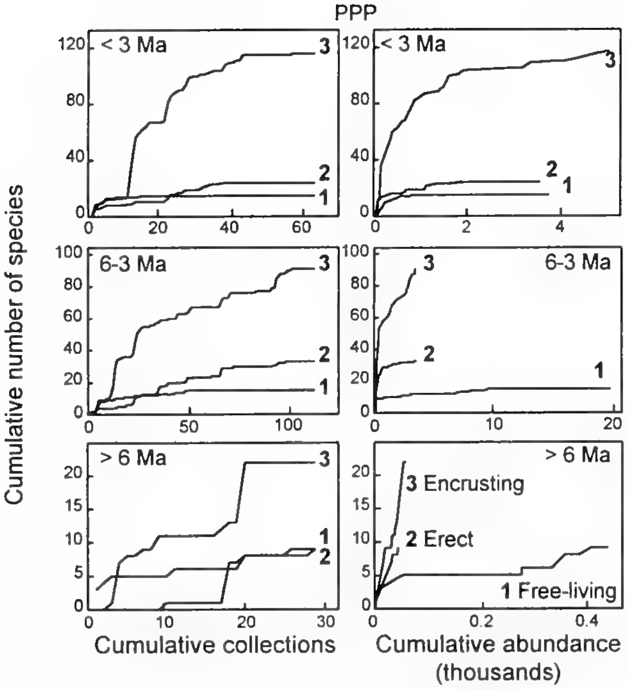
Overall, the encrusting growth form comprises the majority of species in both the PPP (73%) and the DR collections (56%), but only a minority in abundance for both sets of collections (21% in the PPP, 18% in the DR). Consequently, collecting curves for encrusting species (Text-fig. 6) closely reflect the curves for the cheilostome faunas as a whole (Text-fig. 3), *i.e.,* rising stepwise with only a slight tendency for overall flattening. In contrast, the curves for erect and free-living species tend to level off, and to about the same extent for both the PPP and DR collections (Text-fig. 6), implying similarly adequate sampling for species of these growth forms in both areas. However, there are major differences in relative diversity and abundance between the PPP and DR. Erect forms make up 39% of the species and 51% of the abundance in the DR collections, but only 19% of the species and 18% of the abundance in those from the PPP (Text-fig. 6). Even more striking is the difference in the free-living components of the two faunas: 8% of the species and 61% of the abundance in the PPP *versus* 5% of the species and 31% of the abundance in the DR (Text-fig. 6). The virtually complete reversal of relative abundance of free-living and erect species is the most conspicuous difference in the cheilostome faunas of the two areas. Free-living species are almost three times as abundant as either erect or encrusting species in the PPP, whereas erect species are almost twice as abundant as each of the other growth forms in the DR (Text-fig. 6). These patterns probably reflect both temporal and environmental differences between the two areas.



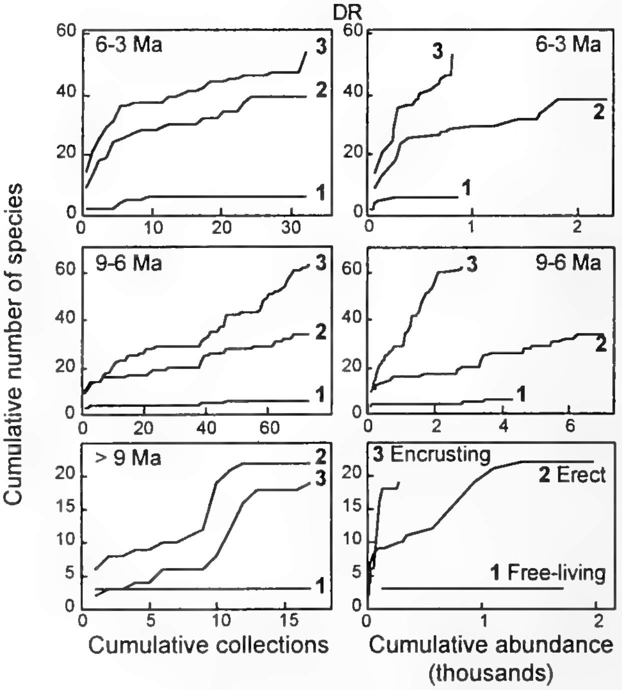
Text-figure 5.—Frequency distributions of numbers of species and abundance per collection for PPP and DR collections.



Text-figure 6.—PPP and DR collecting curves for cheilostome species of three growth forms plotted against numbers of collections and abundance.



Text-figure 7.—PPP collecting curves for cheilostome species of three growth forms in each of three 3-m.y. intervals.



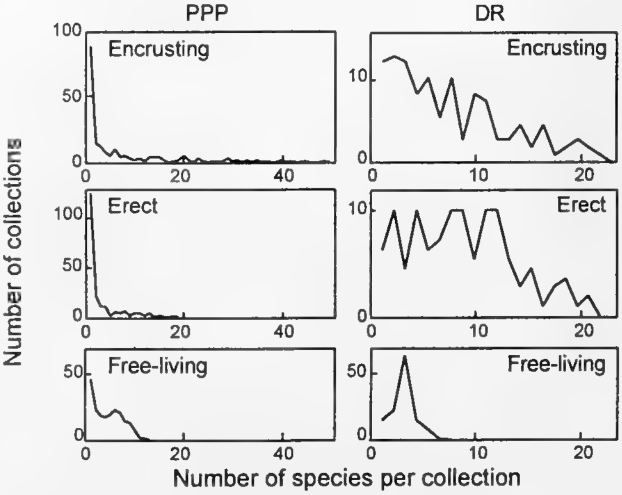
Text-figure 8.—DR collecting curves for cheilostome species of three growth forms in each of three 3-m.y. intervals.

The relative diversities of encrusting, erect, and free-living cheilostomes are maintained in about the same rank order in each of the three 3-m.y. time intervals represented by the PPP collections (Text-fig. 7). However, the number of encrusting species increases from 55% of the total in the oldest interval (>6 Ma) to 65% and finally 75% in the youngest (0–3 Ma). In the youngest interval, the percent share in abundance for the encrusting species more than doubles to 33% (from 13% and 11% in the successively older intervals), partly but not entirely because of the 75% reduction in abundance of free-living species. These changes are probably related to the increased number of reef-associated stratigraphic units sampled in the Late Pliocene–Pleistocene interval in the Bocas and Limon Basins.

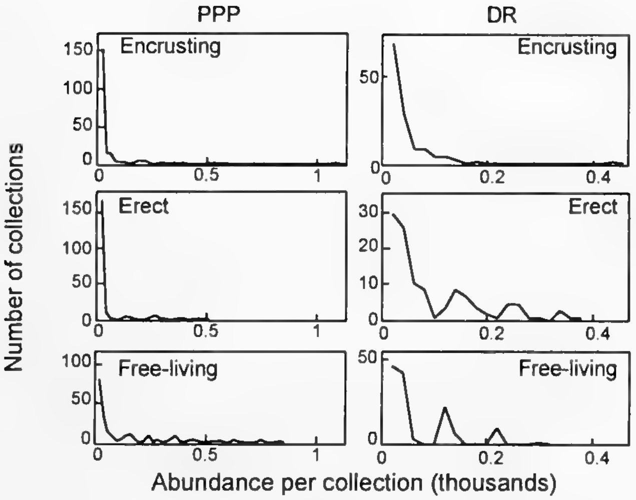
In the DR (Text-fig. 8), the relative diversities and abundances of the three growth forms are more uniform, especially for the 6–3 Ma and 9–6 Ma intervals. The oldest (>9 Ma), however, shows a deficit of encrusting species relative to younger intervals, possibly a sampling artifact. Erect species are dominant in abundance in all three time intervals, comprising 50% or more of the total abundance in each.

Frequency distributions of numbers of species and abundance per collection for each growth form (Text-figs. 9, 10) are similar to those for the faunas as a whole (Text-fig. 5). Modal numbers of species are all one for the PPP and more than one for the DR, with abundances showing less difference between the two areas.

These relationships suggest that sampling adequacy is good to fair for species of different growth forms, and that the quality of sampling is similarly good for the two younger 3-m.y. intervals in each area, and only slightly reduced for the oldest interval in each.



Text-figure 9.—Frequency distributions of numbers of species per collection of three growth forms in the PPP and DR.

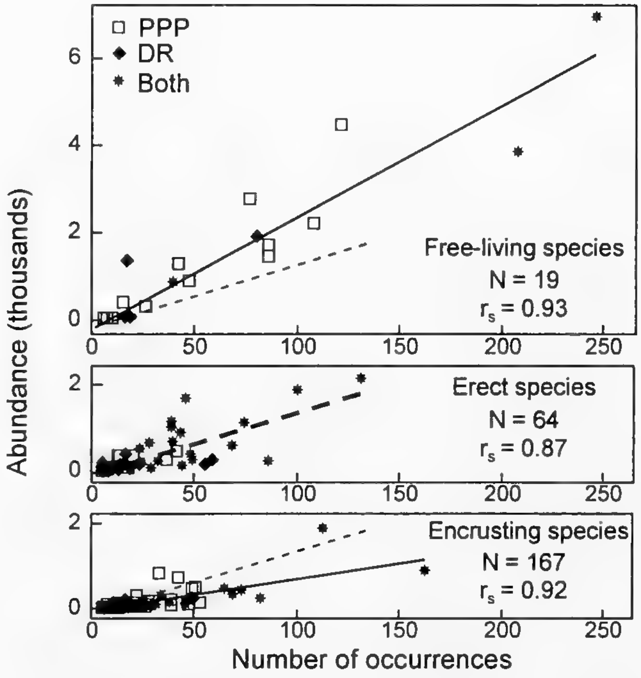


Text-figure 10.—Frequency distributions of abundance per collection of three growth forms in the PPP and DR.

## ABUNDANCE AND OCCURRENCE OF SPECIES

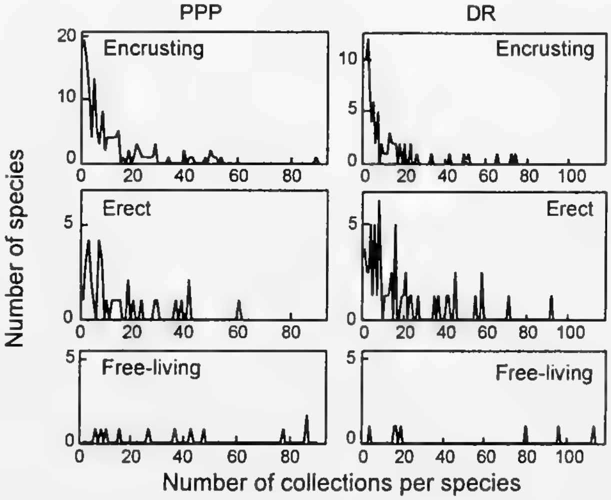
Largely but not entirely because of its superabundance in the PPP collections, free-living growth characterizes the 5 most abundant species in the combined PPP-DR database, and 13 of the 25 most abundant species (Table 3). The same free-living species, *Cupuladria biporosa,* ranks first or second in abundance and number of occurrences in both the PPP and the DR, and is one of only two species to rank in the top 10 in both areas. (The other, *Mamillopora tuberosa,* is also classed as free-living on the basis of morphology illustrated in Cheetham and Jackson, 1999.) The 19 free living species have a median rank in abundance of 14 among the 250 cheilostome species, compared to 79 for the 64 erect species and 152.5 for the 167 encrusting ones. Four free-living species occur in 100 or more collections, in contrast to only two erect and two encrusting ones (Text-fig. 11).

Further differences in the patterns of distribution of the three growth forms are evident in the relationship between the abundance of a species and the number of collections in which it occurs (occurrences; Text-fig. 11). Although abundance is highly significantly correlated with occurrences for all three growth forms (Spearman rank-order correlation 0.87–0.93, $P < 0.001$ in all cases), the rate at which abundance increases with occurrences for free-living species is about 50% greater than the rate of increase for erect species and 100% greater than for encrusting ones (Text-fig. 11). Unsurprisingly, the most frequently occurring and abundant species in each group are those that occur in both the PPP and the DR, although other less common species in each group also occur in both areas (Text-fig. 11).

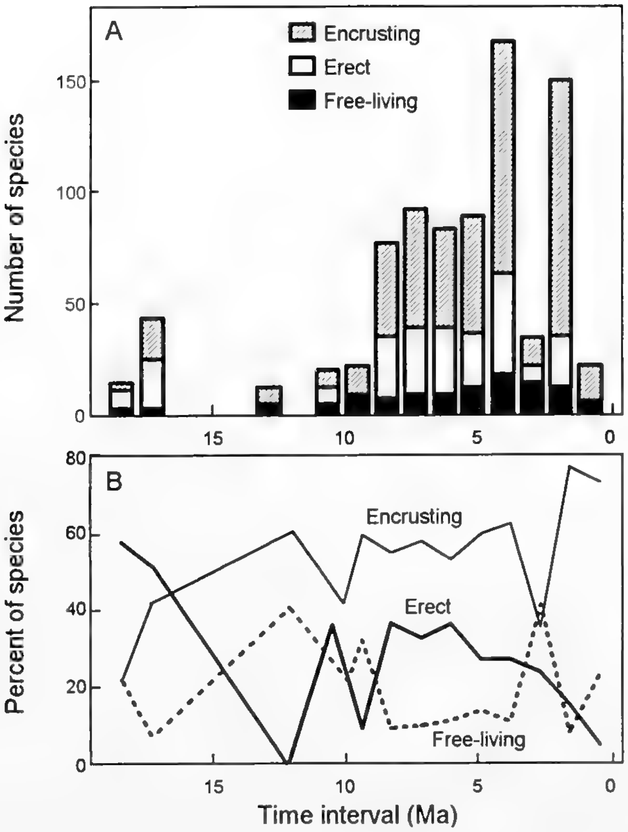


Text-figure 11.—Relationship between total numbers of occurrences ( = number of collections in which each species occurs) and total abundance for 250 cheilostome species in 204 PPP and 124 DR collections. Regressions of abundance on occurrences and Spearman rank-order correlations (all with $P < 0.001$) are shown for each of three growth forms. For comparison of slopes of regression lines, the line for erect species (dashed) is shown on each of the three plots.

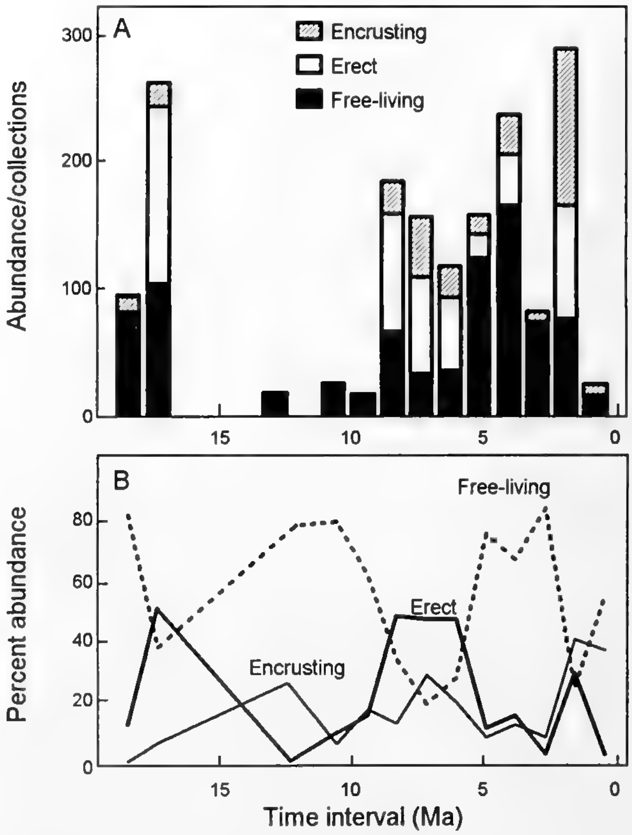
Differences among the three growth forms are also apparent in frequency curves showing the numbers of species with different numbers of occurrences (Text-fig. 12). Encrusting species have strongly unimodal ("hollow") distributions, with 46% occurring in five



Text-figure 12.—Frequency distributions of numbers of collections per species for each of three growth forms in PPP and DR.



Text-figure 13.—Temporal distribution of numbers (A) and percent (B) of species of three growth forms in PPP and DR collections combined. Collections are "binned" in 1-m.y. intervals as in Text-figure 2.



Text-figure 14.—Temporal distribution of abundance (A) and percent abundance (B) of three growth forms in PPP and DR collections combined. Abundance is normalized to the number of collections in each 1-m.y. interval. Collections are "binned" as in Text-figure 2.

or fewer collections (*i.e.*, fewer than 2% of the 328 PPP and DR collections). Only two encrusting species, *Tremogasterina mucronata* and *Biflustra savartii*, are among the 20 most abundant species in the combined dataset, and both are present in both the PPP and the DR collections (Table 3). In marked contrast, free-living species show "flat" frequency curves, *i.e.*, with equal numbers of species having few and many occurrences (Text-fig. 12). The curves for erect species are intermediate in pattern, distinctly less hollow than those for encrusting ones (Text-fig. 12). Only two erect species, *Nellia tenella* and *Thalamoporella biperforata*, both present in both the PPP and DR collections, are among the top ten in abundance in the combined dataset (Table 3).

Frequency curves for the same growth form are strikingly similar between the PPP and DR collections (Text-fig. 12), suggesting that these are inherent properties of species having these growth forms rather than effects of environmental or preservational differences between the two areas. Frequency curves plotted against abundance (not shown) are very similar to those plotted against occurrences (Text-fig. 12), because of the tight correlation between abundance and number of occurrences (Text-fig. 11).

## TEMPORAL DISTRIBUTION OF SPECIES AND GROWTH FORMS

### CHANGES IN RELATIVE IMPORTANCE OF GROWTH FORMS

The distribution of growth forms in the combined PPP-DR database shows two apparent sets of temporal relationships: (1) a rise in numbers of encrusting species and decline in numbers of erect species (Text-fig. 13; Cheetham and Jackson, 1996), and (2) a complementary fluctuation in the relative abundances of erect and free-living species (Text-fig. 14). Confidence in both sets of relationships, however, is affected by the incomplete overlap in the ages of the PPP and DR collections and the small numbers of collections representing several of the 1-m.y. intervals (Text-fig. 2). In addition, the questions of sampling adequacy discussed above make it difficult to judge just how closely differences in numbers of species recovered from different intervals track changes in "true" diversity.

The rise in number of encrusting species and decline in erect forms show considerable fluctuation, much of which appears related to small numbers of samples (Text-fig. 13). The number of free-living species also fluctuates, although with no obvious relationship to the other growth forms (Text-fig. 13). The decline in number of erect species seems fairly steady beginning at 8 Ma, with the sharpest decline beginning at 3 Ma and coinciding with the peak in numbers of encrusting species. Because encrusting diversity may be significantly less adequately sampled than that of other growth forms, much of the apparent fluctuation in the numbers of encrusting species could be sampling artifact. Free-living diversity is much better sampled, and thus fluctuation in species numbers for this growth form should be more meaningful.

Although changes in the abundance of free-living species appear to be complementary to those of erect species (Text-fig. 14), they are also random in time, and appear unrelated to changes in diversity of any of the three growth forms. Despite the strong disparity in abundance of free-living species in the PPP and DR (Text-figs. 7 and 8), the greatest temporal change in free-living abundance occurs within the PPP, between the well-sampled intervals younger and older than 3 Ma (Text-fig. 14).

### TEMPORAL DURATION OF SPECIES

For the 250 species in the combined PPP-DR database, first and last occurrences and estimated ranges are listed in Table 4. First occurrences of 230 species (92%) fall within the database, as do last occurrences of 141 species (56%). With two exceptions (*Metrarabdotos auriculatum,* and *Thalamoporella chubbi*), species whose ranges extend to stratigraphic levels younger than the collections included in the database are still living. Prominent among the still living species not previously known from the fossil record are: *Bracebridgia subsulcata, Semihaswellia sinuosa, Steginoporella connexa, Stylopoma projecta,* and *Tetraplaria dichotoma,* all widely distributed Caribbean species; *Metrarabdotos pacificum* and *M. unguiculatum,* encrusting species of an otherwise erect genus; and *Parasmittina crosslandi, P. fraseri,* and "*Steginoporella*" *cornuta,* common eastern Pacific species. As expected, given the difference in median age between the PPP (3.5 Ma) and DR faunas (7.1 Ma), the proportion of still living species in the PPP (99 of 179, or 55%) is greater than that in the DR (46 of 132, or 35%); the difference is significant statistically (chi-square = 12.78, $P < 0.005$, 1 df).

The median observed stratigraphic range of the 250 species in the PPP-DR database is 3.6 m.y. (Table 4). As an estimate of the actual median duration ("true" range) of the cheilostome fauna as a whole, this value is likely to be biased both by preservation failure at range limits, tending to truncate ranges, and failure of taxa with the shortest durations to be preserved at all, tending to lengthen average range (Foote and Raup, 1996). An additional truncating effect could be expected because of the large number of species ranging to the present, *i.e.*, not yet extinct. However, the median range of the 107 still living species (5.7 m.y.) is actually significantly longer than that of the 143 apparently extinct species (2.1 m.y.) (Mann-Whitney U = 3992, P = 0.0000); thus preservation failure at range limits appears to be a much more significant factor. Given the larger proportion of still living species in the PPP fauna than in the DR, one might expect median ranges of species in the two areas to be different (Text-fig. 15). However, the median observed ranges of species that occur in one area but not the other are not significantly different either among all collections (Mann-Whitney U = 3814, P = 0.3026) or among collections from the well-sampled, 6–3 Ma interval (U = 2345.5, P = 0.8465). These results suggest that, however significant the biases on species durations may be, they are unlikely to apply to the faunas in the two areas differently.

The median stratigraphic range of species occurring in both the PPP and DR collections, however, is highly significantly different from those for species occurring in only one area or the other (Text-fig. 15). With the data for all collections, the median range of the species from both areas (7.8 m.y.) is at least three times that for species from one area alone (2.7 m.y., U = 745, P = 0.0000, for the PPP; 2.0 m.y., U = 587, P = 0.0000, for the DR). The comparisons are much the same for the well-sampled, 6–3 Ma interval (8.0 m.y. for species in both areas; 3.6 m.y., U = 874.5, P = 0.0000, for the PPP; 4.0 m.y., U = 587, P = 0.0000, for the DR). These results are consistent with the correlation between stratigraphic and geographic range noted in *Metrarabdotos* and *Stylopoma* (Cheetham and Jackson, 1996), *i.e.* a lowered probability of extinction with increased geographic range (Jackson, 1974).

In marked contrast, the small differences in median stratigraphic ranges among species with different growth forms (Text-fig. 16) are all nonsignificant (P = 0.0780–0.7470 in Mann-Whitney U tests). Deletion of the two species with extremely long ranges, *Trypostega venusta* and *Nellia tenella,* changes calculated values slightly but leaves the statistical tests unchanged. Thus, stratigraphic ranges (*i.e.*, extinction probabilities) appear to depend much less on the marked differences in patterns of occurrence and abundance among species of different growth forms noted above (Text-figs. 8–11) than on the extent of a species' geographic range.

Table 4.—Stratigraphic ranges and oldest and youngest occurrences of cheilostome bryozoan species present in PPP and DR collections. References in parentheses are for fossil occurrences outside the PPP-DR database.

| Species | Range (m.y.) | Oldest occurrence | Youngest occurrence |
|---|---|---|---|
| *Adeonellopsis deformis* | 4.4 | NMB 16913, 17269; USGS 8525 | NMB 15829 |
| *Adeonellopsis* n. sp. 1 | 7.4 | TU 1293 | Living |
| *Adeonellopsis* n. sp. 2 | 0.0 | NMB 17273 | NMB 17273 |
| *Adeonellopsis* n. sp. 3 | 1.9 | PPP 334, 367, 368 | PPP 710 |
| *Aimulosia palliolata* | 5.3 | NMB 15964 | Living |
| *Alderina smitti* | 3.6 | PPP 370 | Living |
| *Amphiblestrum pustulatum* | 3.1 | NMB 17023 | Living |
| *Antropora granulifera* | 3.6 | PPP 65 | Living |
| *Antropora leucocypha* | 16.2 | (Scolaro, 1968) | Living |
| *Antropora typica* | 5.7 | PPP 183, 391 | Living |
| *Arthropoma cecilii* | 4.3 | PPP 205 | Living |
| n. gen. B n. sp. y | 12.7 | (Scolaro, 1968) | PPP 708, 709, 720, 722, 723 |
| *Bellulopora bellula* | 3.5 | PPP 709 | Living |
| *Biflustra denticulata* | 1.8 | PPP 86 | Living |
| *Biflustra savartii* | 16.0 | NMB 17285 | Living |
| *Bracebridgia subsulcata* | 4.3 | PPP 345 | Living |
| *Buskea* n. sp. 1 aff. *B. dichotoma* | 1.5 | PPP 663 | PPP 644, 653, 943, 944, 948–950, 962, 963 |
| *Caberea* sp. | 1.9 | PPP 68, 720 | PPP 738 |
| *Calpensia* sp. | 0.0 | PPP 86, 137, 144, 146, 156 | PPP 86, 137, 144, 146, 156 |
| *Calyptooecia insidiosa* | 6.6 | NMB 15849 | Living |
| *Canda simplex* | 16.0 | NMB 16935 | Living |
| *Canda* n. sp. | 1.9 | NMB 16817 | NMB 17023 |
| *Cauloramphus* aff. *C. brunea* | 0.0 | PPP 47, 86, 144, 146 | PPP 47, 86, 144, 146 |
| *Cellaria bassleri* | 3.6 | PPP 294, 295, 370 | Living |
| *Cellaria* aff. *C. bassleri* | 2.2 | USGS 8702 | PPP 710 |
| *Cellaria mandibulata* | 7.7 | NMB 15901 | Living |
| *Celleporaria albirostris* | 4.3 | PPP 346, 352 | Living |
| *Celleporaria brunnea* | 16.0 | NMB 16935 | Living |
| *Celleporaria magnifica* | 16.2 | (Scolaro, 1968) | Living |
| *Celleporaria* n. sp. | 0.0 | PPP 352 | PPP 352 |
| *Chaperia condylata* | 16.0 | NMB 17288 | Living |
| *Characodoma contractum* | 16.2 | (Scolaro, 1968) | Living |
| *Cigclisula porosa* | 14.4 | NMB 17283 | PPP 631, 943, 944, 948–950, 962, 963 |
| *Coleopora* aff. *C. americana* | 1.6 | PPP 644, 949, 963 | Living |
| *Coleopora granulosa* | 4.3 | NMB 17175 | NMB 17023 |
| *Copidozoum planum* | 4.3 | PPP 60 | Living |
| *Copidozoum* aff. *C. tenuirostre* | 1.3 | NMB 15903 | NMB 15851 |
| *Corynostylus labiatus* | 12.5 | NMB 17283 | PPP 932 |
| *Crassimarginatella* aff. *C. corbula* | 1.7 | PPP 642 | Living |
| *Crepidacantha longiseta* | 1.6 | PPP 949, 950 | Living |
| *Crepidacantha poissonii* | 4.3 | PPP 60 | Living |
| *Cupuladria biporosa* | 20.0 | (McGuirt, 1941) | Living |
| *Cupuladria* n. sp. 1 aff. *C. biporosa* | 10.0 | PPP 4, 10 | PPP 631, 644, 717, 718, 944, 948–950, 962 |
| *Cupuladria* n. sp. 2 aff. *C. biporosa* | 2.2 | PPP 61 | PPP 177 |
| *Cupuladria* n. sp. 3 aff. *C. biporosa* | 7.0 | PPP 162 | PPP 631, 644, 653, 712, 943, 944, 948–950, 962, 963 |
| *Cupuladria* n. sp. 4 aff. *C. canariensis* | 2.7 | PPP 348, 349 | PPP 631, 644, 653, 712, 944, 948–950, 962 |
| *Cupuladria* n. sp. 5 aff. *C. canariensis* | 2.7 | PPP 350, 352, 422 | PPP 631, 944, 948, 950, 963 |
| *Cupuladria* n. sp. 6 | 8.8 | PPP 1 | PPP 180, 362 |
| *Cycloperiella rubra* | 6.8 | PPP 162 | PPP 47, 86, 144 |
| *Cycloperiella* n. sp. | 0.7 | PPP 205, 346, 348, 350, 352 | PPP 65, 294, 295, 298, 306, 307, 334, 335 |
| *Discoporella* n. sp. 1 | 4.3 | NMB 15916, 17269 | NMB 16865 |
| *Discoporella* n. sp. 2 | 4.1 | NMB 16856 | NMB 17024 |
| *Discoporella* n. sp. 3 | 5.8 | TU 1225 | PPP 631, 962 |
| *Discoporella* n. sp. 4 | 0.7 | NMB 17284 | NMB 16942 |
| *Discoporella* n. sp. 5 | 7.6 | PPP 162 | PPP 822 |
| *Discoporella* n. sp. 6 | 8.9 | PPP 898 | PPP 781, 819–824, 832, 833 |
| *Discoporella* n. sp. 7 | 8.5 | PPP 1, 4, 10 | PPP 663, 668, 570, 691 |
| *Ditaxipora* n. sp. 1 | 6.4 | NMB 16913; USGS 8525 | PPP 711 |
| *Ditaxipora* n. sp. 2 | 0.0 | NMB 15851, 15853 | NMB 15851, 15853 |

Table 4.—Continued.

| Species | Range (m.y.) | Oldest occurrence | Youngest occurrence |
|---|---|---|---|
| *Drepanophora tuberuculatum* | 7.8 | NMB 16916 | Living |
| *Electra biscuta* | 4.3 | PPP 206, 352 | Living |
| *Escharella*? sp. | 0.0 | PPP 210 | PPP 210 |
| *Escharina pesanseris* | 6.7 | NMB 15860 | Living |
| *Escharina porosa* | 7.1 | NMB 16856 | Living |
| *Escharoides costifer* | 16.2 | (Scolaro, 1968) | Living |
| *Escharoides* n. sp. | 2.0 | NMB 15865 | NMB 16818 |
| *Exechonella* cf. *E. antillea* | 0.8 | NMB 15846 | NMB 15838 |
| *Fedora* aff. *F. nodosa* | 4.6 | TU 1294 | NMB 15833 |
| *Floridina antiqua* | 1.8 | PPP 86, 148, 156 | Living |
| *Floridina minima* | 1.4 | (Canu and Bassler, 1923) | PPP 631 |
| *Floridinella parvula* | 3.6 | PPP 306 | Living |
| *Gemellipora* n. sp. 1 | 0.8 | NMB 15823 | NMB 17023 |
| *Gemellipora* n. sp. 2 | 0.8 | NMB 15823 | NMB 17023 |
| *Gemelliporella glabra* | 2.8 | PPP 361 | Living |
| *Gemelliporella punctata* | 8.0 | PPP 35 | PPP 653 |
| *Gemelliporella*? n. sp. | 3.8 | NMB 15962 | PPP 644, 943, 944, 948–950, 962, 963 |
| *Gemelliporidra magniporosa* | 1.8 | PPP 47 | Living |
| *Gemelliporidra multilamellosa* | 3.6 | PPP 65 | Living |
| *Gemelliporidra*? sp. | 4.1 | NMB 15911 | NMB 16865 |
| *Gephyrophora* cf. *G. rubra* | 6.0 | NMB 16834 | Living |
| *Gigantopora fenestrata* | 6.5 | NMB 15851 | Living |
| *Hiantopora intermedia* | 1.6 | PPP 949 | Living |
| *Hincksina* sp. | 0.0 | Olsson 179 | Olsson 179 |
| *Hippaliosina rostrigera* | 16.2 | (Scolaro, 1968) | Living |
| *Hippaliosina* n. sp. | 0.8 | NMB 16915 | NMB 16855 |
| *Hippomenella*? *fissurata* | 2.0 | PPP 65, 298 | PPP 653, 943, 944, 948, 950, 962, 963 |
| *Hippomenella*? aff. *H.*? *fissurata* | 0.6 | NMB 16995 | NMB 16834 |
| *Hippopetraliella* cf. *marginata* | 2.1 | NMB 16856 | NMB 16817 |
| *Hippopleurifera mucronata* | 16.2 | (Scolaro, 1968) | Living |
| *Hippopleurifera* n. sp. 1 | 0.9 | NMB 16833 | NMB 16818 |
| *Hippopleurifera* n. sp. 2 | 0.1 | PPP 710 | PPP 949 |
| *Hippopodina* cf. *H. bernardi* | 1.6 | NMB 15914 | NMB 16835 |
| *Hippopodina feegeensis* | 1.7 | PPP 635 | Living |
| *Hippopodina* aff. *H. feegeensis* | 9.7 | NMB 16935 | NMB 16832 |
| *Hippoporella costulata* | 1.9 | PPP 68, 69, 210, 212, 704, 709, 720 | PPP 631, 738, 944, 950, 962, 963 |
| *Hippoporella gorgonensis* | 16.2 | (Scolaro, 1968) | Living |
| *Hippoporella* aff. *H. rimata* | 2.7 | PPP 205, 206, 352 | PPP 962 |
| *Hippoporidra edax* | 11.6 | PPP 10 | Living |
| *Hippoporina aculeata* | 8.6 | PPP 162 | Living |
| *Hippoporina* n. sp. 1 | 0.7 | PPP 60 | PPP 294, 298 |
| *Hippoporina* n. sp. 2 | 1.8 | PPP 66 | PPP 86, 137, 146 |
| *Hippoporina* n. sp. 3 | 0.0 | PPP 86, 137, 144 | PPP 86, 137, 144 |
| *Jaculina* sp. x | 0.7 | (Scolaro, 1968) | Olsson 179 |
| *Labioporella* aff. *L. dumonti* | 0.0 | PPP 668 | PPP 668 |
| *Labioporella miocenica* | 12.2 | NMB 17286 | USGS 8702 |
| *Labioporella* aff. *L. miocenica* | 0.1 | PPP 634 | PPP 949 |
| *Lagenicella marginata* | 1.7 | PPP 635, 642 | Living |
| *Lagenicella* aff. *L. mexicana* | 2.6 | PPP 312, 367 | PPP 781, 835 |
| *Lagenicella* n. sp. | 1.9 | PPP 210 | PPP 949, 963 |
| *Lagenipora* sp. | 0.1 | PPP 640 | PPP 712 |
| *Mamillopora cavernulosa* | 2.7 | PPP 345, 350, 352, 354 | PPP 738, 940, 944, 950 |
| *Mamillopora tuberosa* | 15.2 | (Scolaro, 1968) | PPP 832, 833 |
| *Mamillopora* n. sp. 1 | 2.0 | PPP 365, 367, 368, 370 | PPP 631 |
| *Mamillopora* n. sp. 2 | 4.1 | PPP 187 | PPP 362 |
| *Margaretta buski* | 16.2 | (Scolaro, 1968) | Living |
| *Margaretta* n. sp. 1 | 12.4 | Olsson 179 | NMB 17023 |
| *Margaretta* n. sp. 2 | 0.1 | NMB 17290 | NMB 17184 |
| *Membraniporella*? sp. | 1.4 | PPP 670 | PPP 634 |
| *Metrarabdotos auriculatum* | 5.7 | NMB 16186 | (Cheetham, 1968) |

Table 4.—Continued.

| Species | Range (m.y.) | Oldest occurrence | Youngest occurrence |
|---|---|---|---|
| *Metrarabdotos colligatum* | 4.2 | TU 1294 | USGS 8702 |
| *Metrarabdotos lacrymosum* | 5.1 | NMB 15915 | PPP 362 |
| *Metrarabdotos pacificum* | 3.6 | PPP 66 | Living |
| *Metrarabdotos tenue* | 4.6 | NMB 17268 | Living |
| *Metrarabdotos unguiculatum* | 5.9 | NMB 16833 | Living |
| *Metrarabdotos* n. sp. 1 | 0.5 | NMB 17284 | NMB 17265 |
| *Metrarabdotos* n. sp. 2 | 0.3 | NMB 17184 | NMB 16942 |
| *Metrarabdotos* n. sp. 3 | 3.9 | NMB 16191 | USGS 8702 |
| *Metrarabdotos* n. sp. 4 | 2.2 | TU 1293 | NMB 15814 |
| *Metrarabdotos* n. sp. 5 | 1.4 | NMB 15911 | NMB 16986 |
| *Metrarabdotos* n. sp. 6 | 0.6 | NMB 16191 | NMB 15878 |
| *Metrarabdotos* n. sp. 7 | 2.2 | TU 1293 | NMB 15814 |
| *Metrarabdotos* n. sp. 8 | 8.0 | PPP 35 | PPP 653 |
| *Metrarabdotos* n. sp. 9 | 3.5 | NMB 17005 | USGS 8702 |
| *Metrarabdotos* n. sp. 10 | 4.5 | NMB 16844 | PPP 214 |
| *Micropora coriacea* | 8.6 | PPP 162 | Living |
| *Microporella* cf. *M. ciliata* | 3.4 | NMB 15851 | NMB 17023 |
| *Microporella normani* | 8.9 | PPP 1152 | PPP 773, 832 |
| *Microporella umbracula* | 5.7 | PPP 391 | Living |
| *Mollia*? sp. | 0.0 | NMB 17023 | NMB 17023 |
| *Monoporella nodulifera* | 4.3 | PPP 352 | Living |
| *Mychoplectra*? sp. | 0.0 | NMB 16995 | NMB 16995 |
| *Nellia tenella* | 65.0 | (Winston and Cheetham, 1984) | Living |
| *Nellia* cf. *N. tenuis* | 8.4 | NMB 17286 | NMB 16929 |
| *Odontoporella adpressa* | 3.6 | PPP 66 | Living |
| *Onychocella* aff. *O. angulosa* | 5.5 | NMB 16811 | PPP 833 |
| *Onychocella* n. sp. | 3.5 | NMB 16856 | NMB 15829 |
| *Parasmittina* aff. *P. areolata* | 8.0 | NMB 17269 | Living |
| *Parasmittina crosslandi* | 4.3 | PPP 206, 350, 532 | Living |
| *Parasmittina fraseri* | 4.3 | PPP 60, 205 | Living |
| *Parasmittina hastingsae* | 3.5 | PPP 68, 69 | Living |
| *Parasmittina* aff. *P. murarmata* | 3.5 | PPP 708, 937 | Living |
| *Parasmittina parsevaliformis* | 15.5 | Olsson 179 | Living |
| *Parasmittina spathulata* | 11.6 | PPP 222 | Living |
| *Parasmittina* n. sp. 1 | 10.0 | PPP 222 | PPP 644, 944 |
| *Parasmittina* n. sp. 2 | 0.9 | NMB 17269 | NMB 16856 |
| *Parasmittina* n. sp. 3 | 15.5 | NMB 17265 | Living |
| *Parasmittina* n. sp. 4 | 0.3 | NMB 16913 | NMB 16928 |
| *Parasmittina* n. sp. 5 | 0.0 | NMB 15842 | NMB 15842 |
| *Parasmittina* n. sp. 6 | 0.0 | NMB 15851 | NMB 15851 |
| *Parasmittina* n. sp. 7 | 0.0 | PPP 631 | PPP 631 |
| *Parasmittina* n. sp. 8 | 4.3 | PPP 205 | Living |
| *Parellisina curvirostris* | 1.7 | PPP 639, 640 | Living |
| *Parkermavella punctigera* | 1.6 | PPP 631, 949 | Living |
| *Pasythea tulipifera* | 3.6 | PPP 64, 65 | Living |
| *Pasythea* n. sp. | 12.8 | NMB 17327 | USGS 8702 |
| *Petraliella bisinuata* | 3.5 | PPP 68, 69, 210–212, 704 | Living |
| *Pleurocodonellina* sp. | 0.0 | PPP 68, 210 | PPP 68, 210 |
| *Poricellaria* n. sp. 1 | 11.8 | NMB 17184 | NMB 15823 |
| *Poricellaria* n. sp. 2 | 0.0 | NMB 16935 | NMB 16935 |
| *Puellina innominata* | 3.5 | PPP 709 | Living |
| *Puellina radiata* | 4.3 | PPP 205, 348, 352 | Living |
| *Puellina* n. sp. aff. *P. radiata* | 1.9 | PPP 69, 708, 709, 723 | PPP 653, 943, 949, 950, 962, 963 |
| *Reptadeonella bipartita* | 4.3 | PPP 205, 352 | Living |
| *Reptadeonella hastingsae* | 15.4 | NMB 16942 | Living |
| *Reptadeonella tubulifera* | 4.3 | PPP 201 | Living |
| *Reptadeonella* n. sp. | 2.9 | NMB 15849 | NMB 15829 |
| *Reteporellina evelinae* | 9.6 | PPP 35 | Living |
| *Retevirgula tubulata* | 3.1 | NMB 17023 | Living |
| *Rhynchozoon* aff. *R. phyrnoglossum* | 0.0 | PPP 148 | PPP 148 |

Table 4.—Continued.

| Species | Range (m.y.) | Oldest occurrence | Youngest occurrence |
|---|---|---|---|
| *Rhynchozoon rostratum* | 4.3 | PPP 206, 207, 352, 355, 422 | Living |
| *Rhynchozoon verruculatum* | 1.8 | PPP 145, 146, 156 | Living |
| *Savignyella* sp. | 12.6 | NMB 17184 | NMB 17023 |
| savignyellid? sp. | 0.2 | NMB 17184 | Olsson 179 |
| *Schedocleidochasma cleidostoma* | 8.6 | PPP 162 | Living |
| *Schedocleidochasma porcellanum* | 16.2 | (Scolaro, 1968) | Living |
| *Schedocleidochasma* n. sp. 1 | 2.6 | PPP 345, 350, 352 | PPP 634 |
| *Schedocleidochasma* n. sp. 2 | 1.9 | PPP 937 | PPP 949 |
| *Schedocleidochasma* n. sp. 3 | 2.7 | PPP 204, 205, 345, 348–350, 352, 354 | PPP 738, 944, 948, 950, 962, 963 |
| *Schizoporella cornuta* | 9.9 | PPP 1171 | Living |
| *Schizoporella floridana* | 4.3 | PPP 419, 422 | Living |
| *Schizoporella magniporosa* | 5.6 | USGS 8525 | PPP 691; NMB 17023 |
| *Scrupocellaria maderensis* | 3.6 | PPP 367 | Living |
| *Scrupocellaria pusilla* | 3.5 | PPP 68 | Living |
| *Scrupocellaria regularis* | 16.2 | (Scolaro, 1968) | Living |
| *Scrupocellaria* aff. *S. unguiculata* | 0.0 | PPP 68, 69, 210 | PPP 68, 69, 210 |
| *Scrupocellaria* n. sp. 1 | 12.4 | Olsson 179 | NMB 17023 |
| *Scrupocellaria* n. sp. 2 | 12.4 | Olsson 179 | NMB 17023 |
| *Semihaswellia sinuosa* | 7.4 | NMB 16910 | Living |
| *Skylonia dohmi* | 0.7 | NMB 17283 | NMB 16942 |
| *Smittina*? n. sp. 1 | 0.0 | PPP 823, 833 | PPP 823, 833 |
| *Smittina*? n. sp. 2 | 0.0 | PPP 944, 963 | PPP 944, 963 |
| *Smittipora* aff. *S. acutirostris* | 5.6 | NMB 15878 | PPP 738, 949, 962, 963 |
| *Smittipora levinseni* | 16.2 | (Scolaro, 1968) | Living |
| *Smittoidea maleposita* | 13.7 | Olsson 179 | PPP 86, 137, 144, 146, 156 |
| *Smittoidea pacifica* | 1.6 | PPP 653, 949 | Living |
| *Smittoidea prolifica* | 1.8 | PPP 86 | Living |
| *Steginoporella magnilabris* | 9.6 | PPP 35 | Living |
| *Steginoporella parvicella* | 6.3 | USGS 8528 | PPP 634 |
| *Steginoporella* n. sp. 1 | 1.5 | NMB 16844 | NMB 16817 |
| *Steginoporella* n. sp. 2 | 0.1 | NMB 16838 | NMB 16836 |
| *Steginoporella* n. sp. 3 aff. *S. connexa* | 10.0 | PPP 222 | PPP 944, 948–950, 962, 963 |
| *Steginoporella* n. sp. 4 aff. *S. connexa* | 0.1 | PPP 640, 710 | PPP 631, 738 |
| "*Steginoporella*" *cornuta* | 7.1 | NMB 16856 | Living |
| *Stylopoma informatum* | 8.0 | USGS 8525 | Living |
| *Stylopoma minutum* | 7.8 | NMB 16916 | Living |
| *Stylopoma projectum* | 3.5 | PPP 722, 723 | Living |
| *Stylopoma spongites* | 16.2 | (Scolaro, 1968) | Living |
| *Stylopoma* n. sp. 3 | 3.5 | PPP 720 | Living |
| *Stylopoma* n. sp. 4 | 1.1 | NMB 15851 | NMB 15962 |
| *Stylopoma* n. sp. 5 | 0.1 | NMB 16928 | NMB 16929 |
| *Stylopoma* n. sp. 6 | 15.5 | Olsson 179 | Living |
| *Stylopoma* n. sp. 7 | 6.5 | NMB 16842 | Living |
| *Stylopoma* n. sp. 11 | 3.6 | PPP 367 | Living |
| *Stylopoma* n. sp. 13 | 7.7 | NMB 16928 | Living |
| *Stylopoma* n. sp. 14 | 6.9 | NMB 15863 | Living |
| *Tetraplaria dichotoma* | 7.1 | NMB 16856 | Living |
| *Thalamoporella biperforata* | 12.4 | Olsson 179 | PPP 672 |
| *Thalamoporella chubbi* | 0.7 | PPP 295 | (Lagaaij, 1959) |
| *Thalamoporella* n. sp. 1 | 1.5 | NMB 16995 | NMB 16817 |
| *Thalamoporella* n. sp. 2 | 10.6 | NMB 16935 | NMB 16818 |
| *Thalamoporella* n. sp. 3 | 10.6 | NMB 16935 | NMB 16817 |
| *Thalamoporella* n. sp. 4 | 0.0 | PPP 35 | PPP 35 |
| *Thalamoporella* n. sp. 5 | 0.0 | PPP 346 | PPP 346 |
| *Thalamoporella* n. sp. 6 | 0.1 | PPP 370 | PPP 708, 709, 720, 722, 723, 937 |
| *Trematooecia aviculifera* | 7.8 | NMB 16916 | Living |
| *Trematooecia* cf. *T. hexagonalis* | 3.4 | NMB 15854, 16811 | NMB 17023 |
| *Trematooecia turrita* | 6.6 | NMB 15849 | Living |
| *Tremagasterina vaughani* | 4.0 | NMB 16916 | USGS 8702 |
| *Tremogasterina mucronata* | 16.2 | (Scolaro, 1968) | Living |

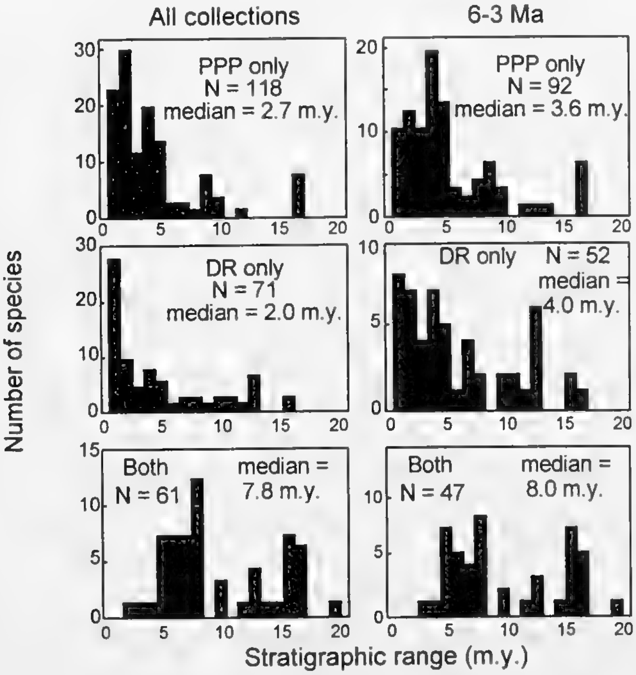
Table 4.—Continued.

| Species | Range (m.y.) | Oldest occurrence | Youngest occurrence |
|---|---|---|---|
| *Tremoschizodina lata* | 1.6 | PPP 631, 738 | Living |
| *Triporula stellata* | 3.1 | PPP 663 | Living |
| *Trypostega venusta* | 35.0 | (Canu and Bassler, 1920) | Living |
| *Trypostega* sp. | 1.4 | NMB 16836 | NMB 16817 |
| *Turbicellepora* n. sp. | 2.7 | PPP 205, 352, 422 | PPP 631, 944, 948, 962, 963 |
| *Vibracellina laxibasis* | 2.7 | PPP 352 | PPP 631, 644, 653, 738, 943, 944, 948–950, 962, 963 |
| *Vibracellina* aff. *V. laxibasis* | 12.6 | NMB 17184 | NMB 17023 |
| *Vincularia* n. sp. | 0.7 | NMB 17285 | NMB 16942 |
| *Vittaticella* sp. | 9.8 | NMB 17184 | NMB 16833 |
| *Watersipora subovoidea* | 1.8 | PPP 148 | Living |

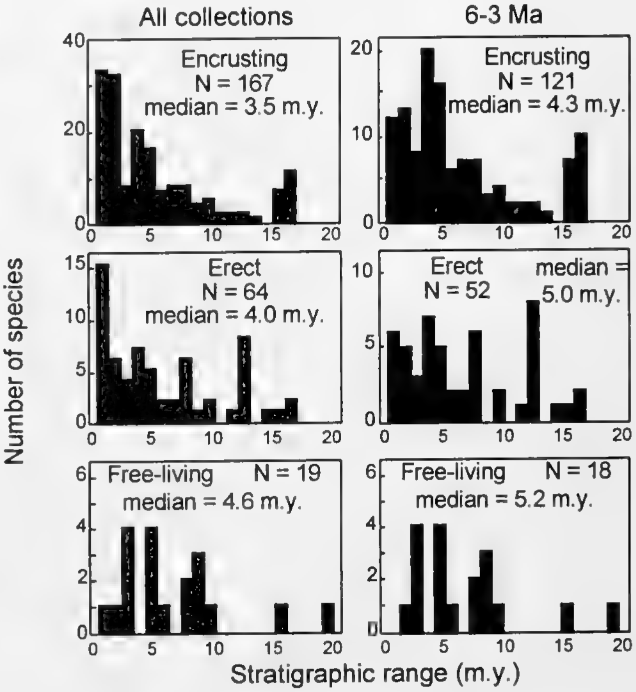
## TEMPORAL DISTRIBUTION OF FIRST OCCURRENCES

The apparent durations of species in the PPP-DR database are affected by incompleteness of temporal overlap between the PPP and DR collections (Text-fig. 2) and by the relatively small proportion of species occurring in both faunas (Text-fig. 15). Fully 66% of the PPP fauna (118 of 179 species) and 54% of the DR fauna (71 of 132 species) do not occur in the other area (the comparable values based only on species in the well-sampled, 6–3 Ma interval are similar: 92 of 139 PPP species, or 66%, and 47 of 99 DR species, or 47%). Nearly half the combined PPP-DR fauna (107 of 250 species, or 43%) range to the present, so the problem of incompleteness is more acute for the distribution of first occurrences than for last occurrences.

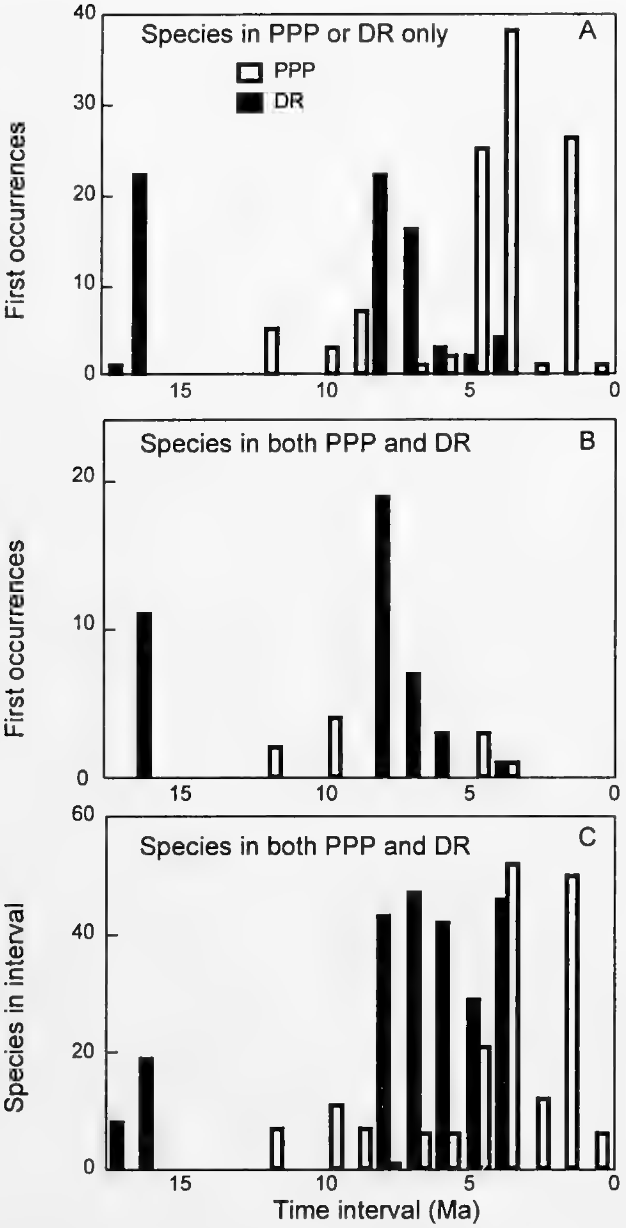
Despite unevenness of sampling, first occurrences that fall within the PPP-DR database are distributed virtually throughout the approximately 16 m.y. represented by the collections (Text-fig. 17). For species occurring in only one area or the other (Text-fig. 17A), significant numbers of first occurrences are distributed



Text-figure 15.—Frequency distributions of observed stratigraphic ranges of cheilostome species occurring only in the PPP or DR, or in both areas. Distributions are shown for all collections (250 species) and for the 6–3 Ma interval that is well-sampled in both areas (191 species). Two extreme outliers, *Trypostega venusta* (35 m.y., PPP only) and *Nellia tenella* (65 m.y., both areas), are not shown.



Text-figure 16.—Frequency distributions of observed stratigraphic ranges of cheilostome species of three growth forms. Distributions are shown for all collections (250 species) and for the 6–3 Ma interval that is well-sampled in both areas (191 species). Two extreme outliers, *Trypostega venusta* (35 m.y., encrusting) and *Nellia tenella* (65 m.y., erect), are not shown.



Text-figure 17.—Temporal distribution of first occurrences of cheilostome species occurring only in the PPP or DR (A, total 189), or in both areas (B, total 61); and the number of species recovered from both areas that were found in each 1-m.y. interval (C). "Binning" is as in Text-figure 2.

through most of the interval from 9 to 3 Ma in both the PPP and DR. More than 60% (73 of 120) of these first occurrences are in the PPP. In contrast, 93% (42 of 45) of the first occurrences of species found in both areas in the 9–3 Ma interval are in the DR (Text-fig. 17B). Despite their strong bias toward first occurrence in the DR, the species that occur in both areas do so in each of the 1-m.y. intervals from 9 Ma to 3 Ma (Text-fig. 17C), suggesting that the biased distribution is not just a sampling artifact. It is tempting to conclude that the bias toward DR first occurrences for these species indicates preferentially westward migration, consistent with the apparent origination of most of the species of *Metrarabdotos* and many of those of *Stylopoma* in the central Caribbean (Cheetham and Jackson, 1996), and with the prevalent direction of near-surface Caribbean circulation. Almost half the species with first occurrences between 9 Ma and 3 Ma in the DR (42 of 89 species, or 47%) are found in the PPP, while only 4% (3 of 76 species) with first occurrences in the same interval in the PPP are found in the DR (Text-fig. 17).

The peaks in apparent originations (Text-fig. 17) at about 8 Ma in the DR (41 species) and at about 4 Ma in the PPP (44 species) coincide approximately with the peaks in origination inferred for *Stylopoma* and *Metrarabdotos* (Cheetham and Jackson, 1996). However, more data are needed to test hypotheses of rates of origination and directions of migration, especially data filling the apparent gap between about 8 Ma and 16 Ma.

## COMPARISON OF PPP AND DR FAUNAS

### GENERAL CHARACTERISTICS

As described above, the PPP fauna is largely younger than that of the DR (Text-fig. 2), richer in species both within areas and for all collections combined (Text-figs. 3, 4), and characterized by greater abundance and diversity of free-living species and lower diversity of erect species (Text-figs. 6–8). Inclusion of collections from the Pacific coast of Panama and Costa Rica (Burica, Golfo Dulce, Nicoya, and Osa regions) appears to be a relatively minor factor in the greater diversity of the PPP collections. Only 10 of 75 species (13%) from the Pacific side of the PPP do not occur on the Caribbean side, compared with the 54% of the DR species (71 of 132) not present in the PPP collections (53% for collections of comparable age in the two areas, *i.e.*, the 6–3 Ma interval). Moreover, only two of the Pacific PPP species, *Smittoidea prolifica* and *Watersipora subovoidea*, that are absent from the Caribbean PPP collections appear to be "true" Pacific species. Others, such as "*Steginoporella*" *cornuta* and *Metrarabdotos pacificum*, formerly known only living in the eastern Pacific, are present in the Caribbean PPP collections. Thus, the percentage of cheilostome species present on both sides of the isthmus since its emergence at about 3.5 Ma may even exceed the 87% shared in the PPP collections; closure of the isthmian seaway appears to have had relatively little evolutionary effect on the cheilostome fauna.

The most significant difference between the PPP and DR faunas is in their contrasting diversity, abundance, and number of occurrences of free-living species (Text-figs. 6–8). In the PPP, such species comprise 58% (7 of 12) of those that occur in 50 or more collections, compared with only 25% (3 of 12) in the DR (Table 3). Although 93% of both PPP (189 of 204) and DR (115 of 124) collections include free-living species, the median abundance of free-living species is 83% of total cheilostome abundance per collection in the PPP but only 28% in the DR. Only 3 of the 7 most abundant free-living species (*Cupuladria biporosa,* ranked 1, *Mamillopora tuberosa,* ranked 3, and *Discoporella* n. sp. 1, ranked 7) occur in the DR, whereas all but one (*Discoporella* n. sp. 1) are present in the PPP collections (Table 3). The 2-to-1 difference in diversity of free-living species (15 in the PPP *versus* 7 in the DR) appears to be real. Despite our attempt to employ the same "splitting philosophy" for collections from both areas, we were able to recognize only 1 species of *Cupuladria,* 4 of *Discoporella,* and 1 of *Mamillopora* in the DR *versus* 7, 4, and 4, respectively, in the PPP.

The ubiquity, abundance, and diversity of free-living species in the PPP fauna are similar to the dominance of such species in bryozoan faunas on the continental margins of North and South America (Marcus and Marcus, 1962; Maturo, 1968; Cadée, 1975; Winston and Håkansson, 1986). However, the morphologically distinctive group of species typified by *Cupuladria doma* appears to be entirely unrepresented in the PPP and DR collections, even though these species are among the most abundant bryozoans living on the continental shelf of the southeastern United States (Winston and Håkansson, 1986), and also occur extensively in Neogene deposits in that area (Cook, 1965; Spencer and Campbell, 1987).

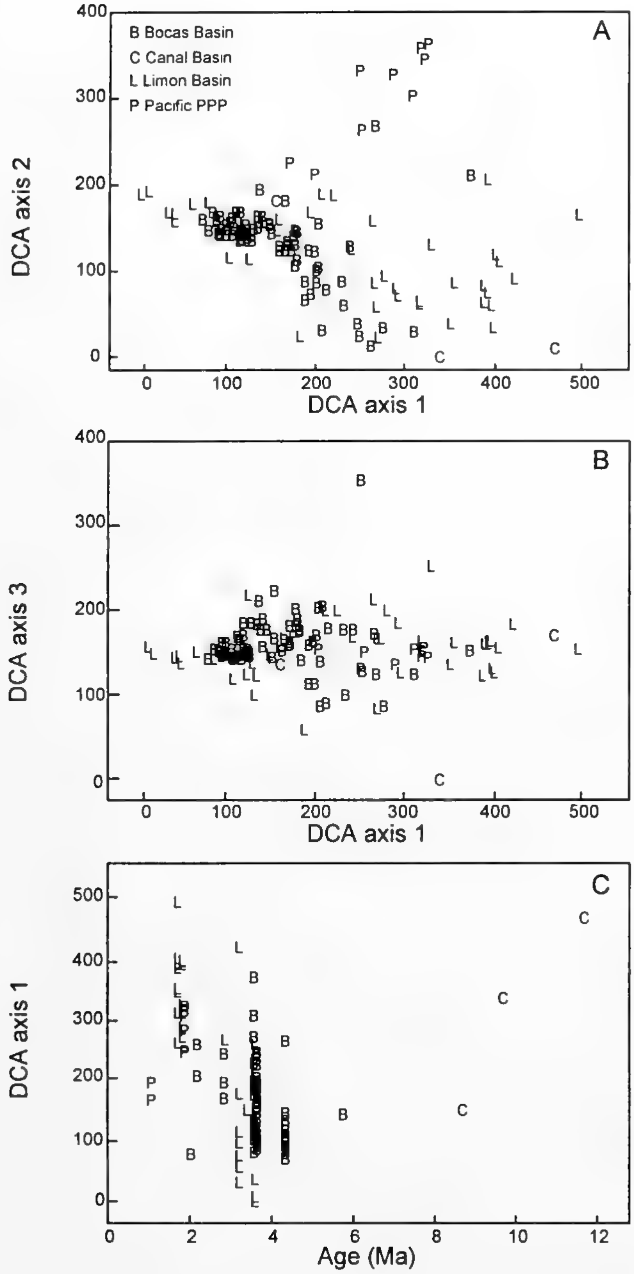
The importance of the erect growth form in the DR fauna stands in marked contrast (Text-fig. 8) to the dominance of free-living forms in the PPP. Almost half (42%, or 5 of 12) of the species that occur in 50 or more collections in the DR are erect, compared to only 8% (1 of 12) of such species in the PPP (Table 3). Only 4 of 124 (3%) collections from the DR lack erect species compared to 86 of 204 (42%) from the PPP. However, erect species are not typically this important in the modern bryozoan fauna of the central Caribbean, where reef-associated species are predominantly encrusting (Jackson and Winston, 1982; Winston and Jackson, 1984). A number of erect genera in the DR collections (*Adeonellopsis, Cigclisula, Gemelliporella,* and *Metrarabdotos*) show abundant evidence of having grown on seagrasses (Cheetham and Jackson, 1996), which were more abundant in the Neogene than they are in the Caribbean today (Ivany *et al.,* 1990). Moreover, recent collecting in the Miocene and Pliocene of Venezuela suggests that faunas dominated by erect species of *Metrarabdotos* and *Schizoporella,* similar to those in the Dominican Republic, may also characterize some Neogene mainland assemblages in sedimentary environments more like those in the Neogene of the DR than the PPP (Jackson and Cheetham, unpublished data).

## QUANTITATIVE DIFFERENCES BETWEEN FAUNAS

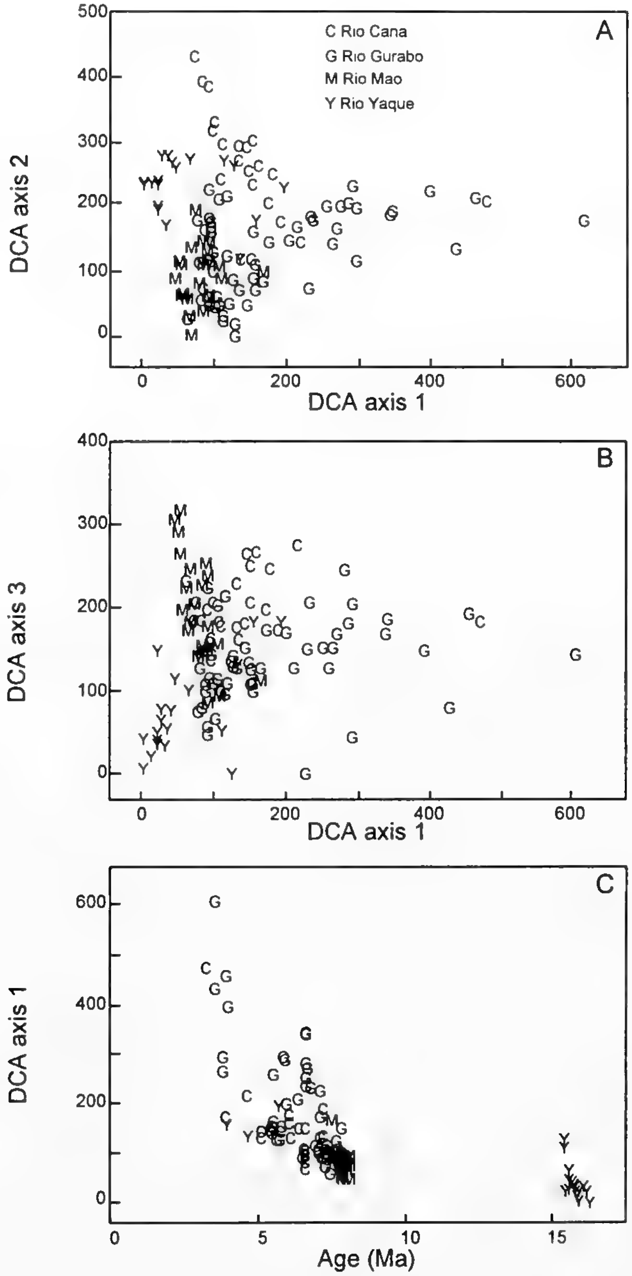
To explore the effects of temporal and spatial influences on the abundance, diversity, and species composition of the PPP and DR cheilostome bryozoans, we used the abundance data from collections (Tables 1, 2) containing six or more species (each of which occurs in at least two collections) in a series of ordination analyses. Separate analyses were made with the PPP (Text-fig. 18) and DR data (Text-fig. 19), and with the two sets of data combined (Text-fig. 20). In each case, detrended correspondence analysis (DCA) was used to relate the differences in species abundances to independent axes of decreasing variation. This technique is a nonparametric analogue of principal components analysis with eigenvectors extracted from a matrix of chi-square distances between collections (McCune and Medford, 1995). Pachut *et al.* (1995) found DCA to be more effective than cluster analysis in ordering abundance data for living Caribbean reef bryozoan assemblages in congruence with water depth. We used PC-ORD version 3.0 to calculate all ordinations; in contrast to earlier versions of detrended correspondence analysis programs, results are no longer dependent on input order of collections or species (McCune and Medford, 1997).

In both the PPP (Text-fig. 18A, B) and the DR (Text-fig. 19A, B) ordinations, collections from the different constituent regions or sections overlap extensively on all three DCA axes. However, there is some separation on DCA axis 2 between PPP collections from the Pacific coast and those from the Caribbean basins (Text-fig. 18A). With the PPP and DR data combined (Text-fig. 20A, B), separation between PPP Pacific and Caribbean collections disappears as the difference between the PPP and DR is emphasized. These results are consistent with percentages of species shared among the three sets of collections, noted above.

To interpret the results of the PPP and DR ordinations, we calculated Spearman rank-order correlations (Table 5) between scores on the DCA axes and (1) the abundance and diversity of colony growth forms in each collection, and (2) the ages and estimated paleodepths for each collection where available (Tables 1, 2). For the DR collections, ages were estimated by



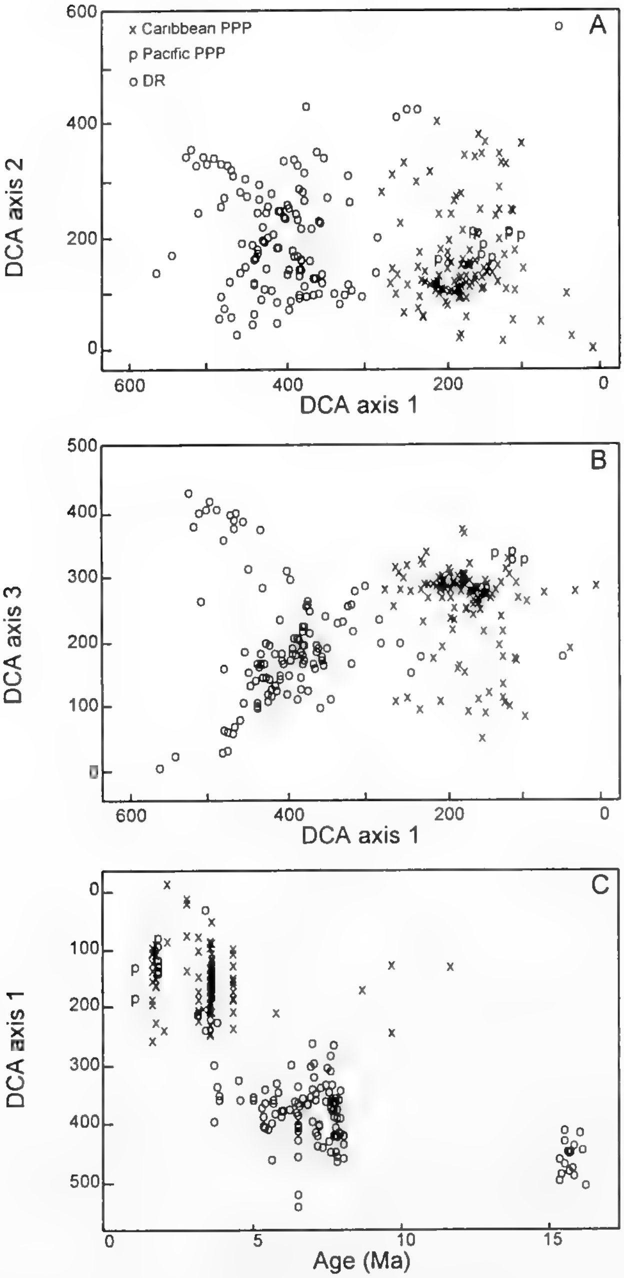
Text-figure 18.—Ordination plots (A, B) of 126 PPP collections (Table 1) on three axes obtained by detrended correspondence analysis (DCA) of abundances (counted as explained in text) of 160 cheilostome species; and (C) relationship between the ages of collections and their scores on DCA axis 1.



Text-figure 19.—Ordination plots (A, B) of 117 DR collections (Table 2) on three axes obtained by detrended correspondence analysis (DCA) of abundances (counted as explained in text) of 120 cheilostome species; and (C) relationship between the ages of collections and their scores on DCA axis 1.

linear interpolation based on stratigraphic thickness between biostratigraphic markers (Saunders *et al.*, 1986; Cheetham, 1986). For the PPP collections, midpoints of age range estimates are from Coates (in Jackson *et al.*, Appendix 1, this volume; written commun., 1998); paleodepths are midpoints of depth ranges based on benthic foraminiferal data (Collins *et al.*, 1995; Collins *et al.*, this volume; Collins in Jackson *et al.*, Appendix 1, this volume).

Highly significant correlations with age (Table 5) suggest that the arrangement on DCA axis 1 in both cases is strongly controlled by temporal changes in species composition and abundance (Text-figs. 18C, 19C). However, the correlation is far stronger for the DR (-0.83) than for the PPP (-0.49; with the three



Text-figure 20.—Ordination plots (A, B) of 126 PPP and 117 DR collections (Tables 1, 2) on three axes obtained by detrended correspondence analysis (DCA) of abundances (counted as explained in text) of 226 cheilostome species; and (C) relationship between the ages of collections and their scores on DCA axis 1. Note that the polarity of DCA axis 1 has been reversed in these plots to enhance comparison with Text-figures 18 and 19.

"outlier" collections from the Canal Basin in Text-fig. 18C deleted, the correlation tightens slightly to −0.56). With collections from the PPP and DR combined, ordination produces a first axis almost as strongly correlated with age as that based on the DR alone (Text-fig. 20C; Spearman correlation 0.78, $P <$ 0.001; the change in polarity of DCA axis 1 scores and in the sign of the correlation coefficient are arbitrary). Thus, a "time's arrow" of changing species composition is evident for the cheilostome fauna as a whole, as well as for that within each area.

The near linearity between axis 1 and age for the DR collections alone (Text-fig. 19C) and for the DR and PPP collections combined (Text-fig. 20C) focuses attention on two sets of "outlier" collections. In the DR, the length of the implied gap, 7–8 m.y. long, between the older samples from the Rio Yaque section (Baitoa Formation) and the oldest ones from the Rio Cana, Rio Gurabo, and Rio Mao sections (Cercado Formation) requires a major decrease in the slope of the otherwise linear trend. The Baitoa has not been dated on planktic foraminiferal or nannofossil evidence (Saunders *et al.,* 1986), so the temporal magnitude of this gap could be less than presently estimated. In the PPP, collections dated at 11.6–8.6 Ma (from the Canal Basin) are much more similar in composition to younger PPP collections than to those nearer their age from the DR (Text-fig. 20C).

Temporal correlation of DCA axis 1 is not only stronger for the DR than for the PPP, but it is also "cleaner" in the sense that none of the other correlations listed in Table 5 are nearly as great. In the PPP, axis 1 is nearly as strongly correlated with paleodepth as with age, and the correlations with most other "environmental" variables (diversity and abundance of different growth forms) are highly significant and in some cases even stronger. In contrast, most of these variables have their highest correlations with DCA axes 2 and 3 in the DR. These relationships suggest that time and environment are less confounded for the DR data than for the PPP. However, a relationship between age and environmental effects is expected for the DR, because stratigraphic sections represent generally deeper-water environments upward (Saunders *et al.,* 1982; Saunders *et al.,* 1986). The difference in sign between correlations of DCA axis 1 with age and paleodepth for the PPP suggests that upward deepening is also true for the PPP, at least for the bryozoan-bearing collections (Table 5).

The ordination analysis thus confirms that temporal differences in the composition of cheilostome faunas are highly significant within the PPP and the DR, and for the combined data set, although temporal and environmental (paleodepth) variables may be in part confounded in both areas. The analysis also confirms the strong similarity between Pacific and Caribbean PPP cheilostome assemblages relative to the much weaker resemblance between the PPP and DR faunas.

Table 5.—Spearman rank-order correlations (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$) between scores on ordination axes and variables of age, paleodepth, diversity and abundance for PPP and DR collections containing six or more species of cheilostome bryozoans (Tables 1 and 2). Axes are from detrended correspondence analysis (DCA).

| | PPP | | | DR | | |
|---|---|---|---|---|---|---|
| Variable | Axis 1 | Axis 2 | Axis 3 | Axis 1 | Axis 2 | Axis 3 |
| Age (Ma) | −0.4949*** | 0.1209 | 0.0010 | −0.8272*** | −0.0650 | −0.2939** |
| Paleodepth (m) | 0.4160*** | −0.3541*** | 0.1554 | | | |
| Number of species | | | | | | |
| Total | 0.5830*** | −0.1395 | 0.0502 | 0.1727 | 0.3831*** | 0.4391*** |
| Encrusting | 0.6207*** | −0.0674 | 0.0307 | 0.2648** | 0.3455*** | 0.6345*** |
| Erect | 0.5485*** | −0.3407*** | −0.0497 | 0.0611 | 0.4106*** | 0.2022* |
| Free-living | −0.1632 | −0.2266* | 0.2980** | −0.1103 | −0.4655*** | −0.2197* |
| Abundance | | | | | | |
| Total | 0.1076 | −0.2313** | 0.0874 | −0.3230*** | 0.1606 | 0.1486 |
| Encrusting | 0.6463*** | −0.2037* | 0.0321 | 0.1216 | 0.2738** | 0.5300*** |
| Erect | 0.5487*** | −0.3488*** | −0.0555 | −0.1731 | 0.4277*** | 0.3512*** |
| Free-living | 0.7754*** | −0.1195 | 0.1930* | −0.4632*** | −0.4950*** | −0.4190*** |

## DISCUSSION

The least expected result of this faunal analysis is the close resemblance between the Neogene cheilostome faunas of the Caribbean and Pacific sides of the Central American isthmus. A possible reason for this similarity is that the time elapsed since closure of the isthmian seaway, at approximately 3.5 Ma, could be significantly shorter than the median duration for these species (the median observed range of 3.6 m.y. is probably no more than 70% of median duration; Cheetham and Jackson, 1998). An additional reason is that a number of species once thought to be characteristic of the eastern Pacific have proven to occur in the Caribbean Neogene, in either PPP or DR collections, or both. The adequacy of sampling for enumerating species distributions both temporally and spatially is an obvious constraint in accepting a hypothesis of such small post-closure change, and the distribution of collections shows clear biases in both time and space. However, numbers of collections and species representing the past 3.5 m.y. are substantial from both sides of the isthmus. Moreover, a different approach to estimating the completeness of representation of taxa, based on the frequency distribution of stratigraphic ranges (Foote and Raup, 1996), suggests that a remarkably high proportion of cheilostome species may have been recovered by the PPP and DR collections (70% to more than 90%, depending on growth form; Cheetham and Jackson, 1998).

Faunal similarity, of course, is relative, and the standard for comparison of the isthmian (PPP) faunas is that of the central Caribbean (DR). The major difference between the cheilostomes of the two areas, the enormous abundance and relatively high diversity of free-living species in the PPP *versus* the relatively high abundance and diversity of erect species in the DR, appears to have both temporal and environmental aspects. Sampling is no doubt biased with regard to both time and environments between the two areas, but diversity estimates for free-living and erect species should be much less affected by such biases than those for encrusting species, because of the major differences in patterns of occurrence and abundance of different growth forms (*i.e.*, "flat" *versus* "hollow" distributions). Thus, the decline in diversity and abundance of erect species seems detectable in both areas, although it appears to have been steepest in the youngest deposits of the PPP. At this stage of characterization of these faunas, it is impossible to go beyond suggesting that the decline may be linked to the growth of erect species on decreasingly available substrata such as seagrass rhizomes (Cheetham and Jackson, 1996).

The fact that, on average, species common to the PPP and DR have stratigraphic ranges (and thus probably "true" durations) about twice as long as those found only in one area or the other is also consistent with the idea that the distance between the two areas was a major determinant in the difference between their faunas. Even given the greater median age of DR collections relative to the PPP, the prevalence of DR first occurrences for species common to the two areas suggests that migration was east to west, consistent with Caribbean near-surface circulation. Sampling bias no doubt plays a part in this result, but the occurrence of these species through much of the interval from 9 Ma to 3 Ma in both areas suggests that the preferential pattern of occurrence is not entirely an artifact.

Whatever the effects of sampling biases, there is a strong component of faunal change ("time's arrow") evident in the highly significant correlation between the ages of collections and the differences in their species composition, both within areas and for the combined data. This result, even by itself, should offer sufficient encouragement for further attempts to disentangle time, space, and environment in the Neogene cheilostome assemblages of tropical America

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## APPENDIX OF SPECIES OCCURRENCES

In the following listing, species are arranged alphabetically in each of the suborders of the Cheilostomatida. A complete systematic listing for these species, following the classification of Gordon (1984, 1986, 1989), along with illustrations of most of the species, is available on the internet, at <http://nmita.geology.uiowa.edu>, the homepage for "Neogene Marine Biota of Tropical America" (NMITA) (Cheetham *et al.*, 1998). For each species, occurrences are arranged numerically under PPP and DR groupings. For the DR occurrences, NMB (Naturhistorisches Museum Basel, Switzerland), TU (Tulane University), and USGS (U. S. Geological Survey) localities are listed and described in Saunders *et al.* (1986); the Olsson localities are in Vokes (1979). The occurrence data are available at the PPP internet site http://www.fiu.edu/~collinsl/. As systematic studies are completed, all specimens will be deposited in the National Museum of Natural History, Washington, D. C.

### Order CHEILOSTOMATIDA Busk, 1852
### Suborder MALACOSTEGINA Levinsen, 1902

***Biflustra denticulata*** Smitt, 1873: **PPP** 86, 712.

***Biflustra savartii*** (Audouin, 1826): **PPP** 34, 47, 58, 63–66, 68, 69, 74, 86, 144, 146, 148, 156, 162, 188, 194, 197, 198, 203, 205–207, 210–212, 214, 294, 295, 298, 306–308, 312, 326, 334, 335, 340, 341, 345, 346, 350, 352, 354, 355, 365, 370, 379, 419, 422, 631, 640, 671–673, 677, 679, 681, 683–685, 691, 695, 697, 704, 708, 709, 712, 720, 722, 723, 820, 822, 824, 832, 833, 835, 896, 907, 932, 933, 937, 939, 946, 975, 1142, 1163, 1164. **DR** NMB 15804, 15814, 15815, 15835–15838, 15842, 15865, 15869, 15878, 15882, 15896, 15897, 15900, 15901, 15903, 15904, 15906, 15907, 15910–15912, 15914–15916, 15934, 15962, 16191, 16192, 16802, 16818, 16828, 16838, 16839, 16842, 16844, 16855, 16857, 16910, 16912–16918, 16922–16924, 16926–16930, 16932, 16935, 16936, 16942, 16995, 17184, 17265, 17268, 17269, 17285–17290, 17327; Olsson 179; TU 1294, 1379; USGS 8525.

***Corynostylus labiatus*** Canu and Bassler, 1919: **PPP** 326, 896, 898, 932. **DR** NMB 15903, 15906, 15907, 15910, 16913, 16915–16918, 16922–16924, 16926–16929, 16935, 16936, 16938, 16942, 17184, 17190, 17265, 17269, 17283, 17285–17290, 17307, 17327; Olsson 179; TU 1294, 1379; USGS 8525.

***Electra biscuta*** Osburn, 1950: **PPP** 144, 148, 206, 352, 933.

***Mychoplectra***? species: **DR** NMB 16836–16839.

## Suborder FLUSTRINA Smitt, 1867

***Alderina smitti*** Osburn, 1950: **PPP** 47, 148, 370.

***Amphiblestrum pustulatum*** (Canu and Bassler, 1928): **DR** NMB 17023.

***Amphiblestrum***? species: **DR** NMB 17023.

***Antropora granulifera*** (Hincks, 1880): **PPP** 65, 86, 146, 148, 738.

***Antropora leucocypha*** (Marcus, 1937): **PPP** 47, 66–69, 86, 137, 144, 146, 148, 162, 198, 206, 207, 294, 295, 298, 306, 346, 352, 354, 379, 631, 639, 642, 705, 709, 710, 950. **DR** NMB 15835, 15851, 15874, 15881, 15882, 15916, 16817, 16818, 16828, 16832, 16833, 16835–16838, 16842, 16857, 16865.

***Antropora typica*** (Canu and Bassler, 1928): **PPP** 47, 63, 65, 66, 68, 69, 86, 144, 148, 183, 193, 204, 205, 210, 211, 295, 307, 334, 352, 391, 631, 634, 639, 640, 653, 704, 705, 709, 712, 722, 723, 738, 943, 944, 948–950, 962, 963.

***Caberea*** species: **PPP** 68, 631, 720, 738.

**calloporid** species: **PPP** 824, 1163, 1164.

***Calpensia*** species: **PPP** 86, 137, 144, 146, 156.

***Canda simplex*** Busk, 1884: **PPP** 35, 68, 86, 210–212, 334, 349, 631, 634, 635, 642, 653, 663, 705, 709, 710, 720, 722, 723, 738, 943, 944, 948–950, 962, 963. **DR** NMB 15805, 15823, 15827, 15828, 15837, 15934, 15962, 16817, 16818, 16832–16835, 16927, 16929, 16935, 17023, 17268; Olsson 179; USGS 8525, 8702.

***Canda*** new species [small zooids]: **DR** NMB 15823, 16817, 17023.

***Cauloramphus*** aff. ***C. brunea*** Canu and Bassler, 1930: **PPP** 47, 86, 144, 146.

***Cellaria bassleri*** Hastings, 1947: **PPP** 68, 178, 180, 210, 294, 295, 358, 362, 370, 639, 640, 663, 704, 738, 943, 944, 950, 963.

***Cellaria*** aff. ***C. bassleri*** Hastings, 1947: **PPP** 367, 708, 709, 710, 720, 722, 723. **DR** NMB 15832, 15833; USGS 8702.

***Cellaria mandibulata*** Hincks, 1882: **PPP** 211, 295, 298, 350, 634, 635, 640, 642, 644, 649, 653, 663, 709, 720, 722, 723, 943, 944, 948, 949, 950, 962, 963. **DR** NMB 15804, 15805, 15814, 15828, 15837, 15842, 15846, 15849, 15860, 15863, 15901, 15934, 15962, 15964, 16810, 16817, 16818, 16828, 16842, 17023.

***Chaperia condylata*** Canu and Bassler, 1930: **PPP** 709. **DR** NMB 16832, 16833, 17023, 17288; Olsson 179.

***Copidozoum planum*** (Hincks, 1880): **PPP** 60, 66, 86, 144, 146, 156.

***Copidozoum*** aff. ***C. tenuirostre*** (Hincks, 1880): **DR** NMB 15851, 15897, 15903, 15906, 16928.

***Crassimarginatella*** aff. ***C. corbula*** (Hincks, 1880): **PPP** 642.

***Crassimarginatella*** species: **PPP** 156, 709, 950, 963.

***Cupuladria biporosa*** Canu and Bassler, 1923: **PPP** 1, 42, 57, 58, 61, 62, 65–69, 71, 72, 74, 86, 137, 144, 161, 162, 184, 187–189, 191, 193–208, 210, 212–214, 294, 295, 298, 306–308, 311, 312, 326, 334, 335, 340, 341, 345, 346, 348–350, 352, 354, 355, 357, 362, 367, 368, 370, 379, 391, 419, 422, 423, 425, 426, 631, 634, 635, 639, 668–672, 675–679, 681–684, 688, 689, 691, 695, 697, 704–709, 712, 720, 722, 723, 738, 773, 820, 822, 832, 833, 907, 908, 916, 931, 932–935, 937, 939, 940, 943, 962, 963, 1134, 1137, 1142, 1145, 1163, 1171. **DR** NMB 15804, 15805, 15814, 15815, 15823, 15829, 15833, 15835, 15836, 15838, 15840, 15842, 15849, 15854, 15860, 15863–15865, 15869, 15871, 15873, 15874, 15876, 15878, 15881, 15882, 15890, 15895–15897, 15900, 15901, 15903, 15904, 15906, 15907, 15910–15916, 15929, 15934, 15936, 15937, 15939, 15947, 15962, 15964, 15966, 15982, 16103, 16167, 16186, 16191, 16192, 16802, 16810, 16817, 16818, 16824, 16828, 16832–16839, 16842, 16844, 16854–16857, 16862, 16865, 16910, 16912–16918, 16922–16924, 16926–16930, 16932, 16935, 16936, 16938, 16942, 16961, 16973, 16985, 16995, 17023, 17175, 17184, 17190, 17265, 17268, 17269, 17283–17290, 17322, 17327; Olsson 179, 180; TU 1225, 1227A, 1293, 1294; USGS 8525, 8702.

***Cupuladria*** new species **1** aff. ***C. biporosa*** Canu and Bassler, 1923 [medium zooids]: **PPP** 4, 10, 34, 57, 60, 61, 63–69, 74, 162, 178, 194–196, 198, 204, 207, 210, 212, 214, 294, 295, 298, 306–308, 311, 312, 326, 334, 335, 340, 341, 345, 346, 348–350, 352, 354, 355, 357, 358, 361, 362, 365, 367, 368, 370, 423, 631, 635, 639, 640, 642, 644, 663, 668, 683, 684, 688, 709, 710, 717, 718, 720, 722, 723, 944, 948–950, 962.

***Cupuladria*** new species **2** aff. ***C. biporosa*** Canu and Bassler, 1923 [small to medium, flat colonies; small zooids]: **PPP** 52, 53, 57, 61, 63, 65, 66, 71, 177, 193.

***Cupuladria*** new species **3** aff. ***C. canariensis*** (Busk, 1859) [large zooids]: **PPP** 53, 57, 63, 64, 66–72, 74, 162, 177, 178, 180, 187, 193–198, 200–208, 210, 212, 213, 294, 295, 298, 306–308, 311, 326, 334, 335, 340, 341, 345, 346, 348–350, 352, 354, 355, 357, 358, 362, 365, 367, 368, 370, 379, 391, 419, 422, 423, 425, 426, 631, 634, 635, 639, 640, 642, 644, 653, 669, 670, 676, 679, 689, 695, 697, 704–706, 708–710, 712, 720, 722, 723, 738, 931–935, 937, 940, 943, 944, 948–950, 962, 963.

***Cupuladria*** new species **4** aff. ***C. canariensis*** (Busk, 1859): **PPP** 57, 68, 69, 74, 178, 180, 193, 194, 197, 198, 210, 334, 340, 348, 349, 357, 361, 362, 365, 367, 368, 370, 631, 634, 635, 639, 640, 642, 644, 645, 653, 678, 695, 697, 704, 708–710, 712, 720, 722, 723, 944, 948–950, 962.

***Cupuladria*** new species **5** aff. ***C. canariensis*** (Busk, 1859) [colony with large basal pores; medium zooids]: **PPP** 68, 69, 198, 210, 212, 306, 308, 350, 352, 361, 362, 367, 368, 370, 422, 631, 635, 639, 640, 720, 722, 723, 944, 948, 950, 963.

***Cupuladria*** new species **6** [colonies with very few basal pores; large zooids]: **PPP** 1, 68, 69, 180, 350, 362.

***Discoporella*** new species **1** [growth determinate, regeneration rare; zooids large; cryptocyst with central pores; opesia with pair of small denticles]: **DR** NMB 15804, 15805, 15809, 15812, 15814, 15815, 15823, 15835, 15836, 15842, 15846, 15860, 15863–15865, 15869, 15871, 15873, 15874, 15876, 15878, 15881, 15882, 15890, 15895–15897, 15900, 15901, 15903, 15904, 15906, 15907, 15910–15912, 15914–15916, 15929, 15933, 15934, 15936–15944, 15946, 15947, 15952, 15962, 15964, 15965, 15968, 15969, 16167, 16186, 16191, 16192, 16802, 16810, 16817, 16818, 16824, 16827, 16828, 16837, 16838, 16842, 16854, 16856, 16857, 16859, 16860, 16862, 16865, 16879, 16910, 16912–16918, 16922–16924, 16926–16930, 16932, 17175, 17268, 17269; TU 1225, 1227A, 1293, 1294; USGS 8525, 8702.

***Discoporella*** new species **2** [growth determinate, regeneration rare; colony base concave; zooids small; cryptocyst without central pores; opesia smooth]: **DR** NMB 15804, 15805, 15809, 15812, 15814, 15815, 15835, 15838, 15860, 15864, 15865, 15869, 15874, 15934, 15944, 15946, 15952, 15962, 15964, 16810, 16854, 16856, 17024.

***Discoporella*** new species **3** [like *D.* n. sp. 2, but with filled colony base]: **PPP** 55, 65, 67–69, 74, 178, 180, 205, 210, 212, 295, 298, 308, 335, 340, 341, 345, 348–350, 352, 362, 365, 367, 368, 370, 631, 668–670, 676, 678, 708, 937, 962. **DR** NMB 15835, 16865; TU 1225; USGS 8702.

***Discoporella*** new species **4** [growth indeterminate, regeneration common; zooids small; cryptocyst rarely with central pores; opesia with many fine denticles]: **DR** NMB 16935, 16936, 16938, 16942, 17184, 17190, 17265, 17283–17290, 17322, 17327; Olsson 179.

***Discoporella*** new species **5** [colonies flat; basal surface smooth; zooids small]: **PPP** 65–67, 71, 72, 74, 146, 162, 194, 195, 198, 200–208, 212–214, 294, 295, 298, 307, 308, 326, 334, 335, 340, 341, 345, 346, 348–350, 352, 355, 362, 368, 376, 379, 391, 419, 422, 423, 425, 426, 668–672, 675–677, 679, 681–685, 688, 689, 691, 695, 697, 705, 706, 708, 709, 720, 722, 723, 822, 931–935, 937, 939, 948.

***Discoporella*** new species **6** [growth determinate; zooids large; cryptocyst without central pores]: **PPP** 47, 53, 55, 57, 58, 61, 63–69, 71, 72, 74, 148, 156, 162, 177, 178, 180, 187, 188, 193–199, 202–208, 210–212, 294, 295, 298, 306–308, 311, 312, 326, 334, 335, 340, 341, 345, 346, 348–350, 352, 354, 355, 357, 358, 362, 365, 367, 368, 370, 379, 391, 419, 422, 423, 425, 426, 631, 634, 635, 639, 640, 642, 644, 645, 649, 668–670, 678, 679, 691, 697, 704–706, 708–710, 712, 720, 722, 723, 773, 781, 818–824, 832, 833, 898, 932, 937, 939, 940, 943, 944, 948–950.

***Discoporella*** new species **7** [zooids medium; basal surface finely pitted; cryptocyst with few central pores]: **PPP** 1, 4, 10, 34, 39, 42, 57, 64–69, 72, 74, 89, 91, 144, 146, 162, 193–198, 201–208, 210, 211, 294, 295, 298, 306–308, 311, 312, 326, 334, 335, 340, 341, 345, 346, 348–350, 352, 355, 357, 368, 379, 422, 423, 425, 426, 663, 668, 670, 679, 691, 704, 708, 709, 720, 722, 723, 932, 933, 939, 940, 1137, 1139, 1142, 1145, 1155, 1163, 1164, 1171.

***Floridina antiqua*** (Smitt, 1873): **PPP** 86, 148, 156.

***Floridina minima*** Canu and Bassler, 1923: **PPP** 631.

***Floridinella parvula*** Canu and Bassler, 1928: **PPP** 47, 86, 156, 210, 308, 635, 663, 670, 818, 944, 950, 962, 963.

***Hiantopora intermedia*** Kirkpatrick, 1890: **PPP** 949.

***Hincksina*** species: **DR** Olsson 179.

***Labioporella*** aff. ***L. dumonti*** (Canu and Bassler, 1928): **PPP** 668.

***Labioporella miocenica*** (Canu and Bassler, 1919): **DR** NMB 15814, 15842, 15849, 15860, 15863, 15869, 15871, 15873, 15876, 15878, 15882, 15890, 15900, 15911, 15912, 15914, 15915, 15934, 15962, 15964, 16167, 16802, 16817, 16818, 16828, 16832–16839, 16842, 16855–16857, 16910, 16916, 16926–16929, 16983, 16989, 17005, 17175, 17268, 17269, 17286; Olsson 180; TU 1293; USGS 8702.

***Labioporella*** aff. ***L. miocenica*** (Canu and Bassler, 1919): **PPP** 634, 949.

***Micropora coriacea*** (Johnston, 1847): **PPP** 137, 162, 207, 307, 653.

***Mollia***? species: **DR** NMB 17023.

***Monoporella nodulifera*** Hincks, 1881: **PPP** 65, 352, 720.

***Nellia tenella*** (Lamarck, 1816): **PPP** 53, 57, 63–66, 68, 69, 144, 162, 171, 178, 180, 193–195, 197, 198, 206, 207, 210–212, 295, 298, 312, 326, 334, 340, 345, 346, 348–350, 354, 355, 357, 365, 367, 370, 631, 634, 635, 653, 679, 697, 705, 709, 712, 720, 722, 723, 908, 932–934, 937, 939, 948, 962. **DR** NMB 15814, 15815, 15837, 15842, 15846, 15849, 15860, 15876, 15878, 15900, 15901, 15903–15907, 15910–15912, 15934, 15962, 16167, 16186, 16817, 16818, 16828, 16832–16839, 16842, 16844, 16856, 16857, 16913, 16916–16918, 16922, 16924, 16926–16930, 16935, 16936, 16938, 16942, 16995, 17184, 17190, 17265, 17268, 17269, 17283, 17285–17290, 17307, 17327; Olsson 179, 180; TU 1294; USGS 8525, 8702.

***Nellia*** cf. ***N. tenuis*** Harmer, 1926: **DR** NMB 15914, 15915, 16916, 16929, 16935, 17184, 17286, 17327.

***Onychocella*** aff. ***O. angulosa*** Reuss, 1847: **PPP** 47, 67, 86, 137, 144, 146, 156, 634, 635, 639, 644, 645, 710, 833, 943, 948–950, 962, 963. **DR** NMB 15851, 15853, 16811.

***Onychocella*** new species **1** [small zooids]: **DR** NMB 15823, 15829, 15851, 15853, 15962, 16811, 16856.

***Parellisina curvirostris*** (Hincks, 1862): **PPP** 639, 640, 944, 949, 950.

***Poricellaria*** new species **1** [*P.* aff. *P. ratoniensis* (Waters, 1887) of Cheetham, 1973]: **DR** NMB 15823, 16817, 16935, 16942, 17184; Olsson 179.

***Poricellaria*** new species **2**: **DR** NMB 16935.

***Retevirgula tubulata*** (Hastings, 1930): **PPP** 47, 86, 144, 146, 156, 949. **DR** NMB 17023.

***Scrupocellaria maderensis*** Busk, 1860: **PPP** 367, 948, 962.

***Scrupocellaria pusilla*** (Smitt, 1872): **PPP** 68, 631, 943, 944, 948, 949, 962, 963.

***Scrupocellaria regularis*** Osburn, 1940: **PPP** 53, 65, 66, 68, 86, 137, 144, 146, 156, 180, 210, 211, 295, 298, 312, 341, 350, 352, 370, 631, 634, 635, 679, 705, 708, 709, 720, 722, 723, 738, 773, 832, 833, 932, 933, 937, 939, 943, 944, 949, 962.

***Scrupocellaria*** aff. ***S. unguiculata*** Osburn, 1950: **PPP** 68, 69, 210.

***Scrupocellaria*** new species **1** [large zooids]: **PPP** 35, 65, 211, 212, 720, 722, 723. **DR** NMB 15815, 15823, 15828, 15837, 15838, 15842, 15849, 15860, 15864, 15900, 15901, 15903, 15904, 15910–15912, 15914, 15915, 15962, 16817, 16818, 16828, 16832, 16833, 16836, 16856, 16857, 16865, 16916, 16918, 16924, 16935, 16936, 16942, 17023, 17184, 17190, 17268, 17269; Olsson 179; USGS 8525.

***Scrupocellaria*** new species **2** [small zooids]: **DR** NMB 15823, 15828, 15838, 15964, 16817, 16818, 16828, 16833, 16838, 16935, 17023, 17184; Olsson 179.

***Skylonia dohmi*** (Sandberg, 1962): **DR** NMB 16935, 16936, 16938, 16942, 17184, 17190, 17265, 17283, 17285–17290, 17327; Olsson 179.

***Smittipora*** aff. ***S. acutirostris*** (Canu and Bassler, 1928): **PPP** 47, 86, 144, 710, 738, 949, 962, 963. **DR** NMB 15878, 16855.

***Smittipora levinseni*** (Canu and Bassler, 1917): **PPP** 50, 65, 66, 86, 144, 146, 148, 156, 162, 205, 294, 295, 298, 308, 334, 340, 352, 634, 670, 709, 723, 944.

***Steginoporella magnilabris*** (Busk, 1854): **PPP** 35, 65, 66, 68, 69, 210–212, 222, 367, 653, 663, 685, 704, 708–710, 712, 720, 722, 723, 933, 948–950, 962, 963. **DR** NMB 16855, 16857.

***Steginoporella parvicella*** (Canu and Bassler, 1919): **PPP** 203, 308, 334, 335, 340, 345, 634, 679. **DR** NMB 15804, 15805, 15814, 15815, 15829, 15835, 15837, 15838, 15842, 15846, 15849, 15854, 15860, 15864, 15865, 15869, 15871, 15876, 15878, 15881, 15882, 15900, 15906, 15911, 15912, 15914, 15915, 15934, 15962, 15964, 16167, 16186, 16192, 16810, 16811, 16817, 16818, 16828, 16832–16834, 16842, 16855–16857, 16865, 16910, 16913–16918, 16922–16924, 16926–16930, 17175, 17269; Olsson 180; TU 1379; USGS 8525.

***Steginoporella*** new species **1**: **DR** NMB 16817, 16818, 16828, 16832–16839, 16842, 16844, 16856, 16857, 16995.

***Steginoporella*** new species **2**: **DR** NMB 16836–16838.

***Steginoporella*** new species **3** aff. ***S. connexa*** (Harmer, 1900): **PPP** 222, 634, 635, 639, 642, 645, 944, 948–950, 962, 963.

***Steginoporella*** new species **4** aff. ***S. connexa*** (Harmer, 1900): **PPP** 631, 640, 710, 738.

***"Steginoporella" cornuta*** Osburn, 1950: **PPP** 47, 86, 257, 704, 720. **DR** NMB 16856.

***Thalamoporella biperforata*** (Canu and Bassler, 1919): **PPP** 74, 672, 684, 704, 708, 709, 720, 722. **DR** NMB 15804, 15805, 15814, 15815, 15832, 15835, 15842, 15846, 15849, 15860, 15863–15865, 15869, 15873, 15876, 15878, 15881, 15882, 15890, 15895–15897, 15900, 15901, 15903, 15904, 15906, 15907, 15910–15916, 15934, 15962, 15964, 16167, 16186, 16192, 16810, 16817, 16818, 16828, 16832–16834, 16836–16839, 16841, 16842, 16844, 16846, 16852, 16855–16857, 16879, 16910, 16912–16918, 16922–16924, 16926–16930, 16932, 16935, 16936, 16938, 16942, 16959, 16961, 16971, 16972, 16988, 16995, 17004, 17175, 17184, 17190, 17265, 17268, 17269, 17278, 17288, 17327; Olsson 179; TU 1379; USGS 8525, 8702.

***Thalamoporella chubbi*** Lagaaij, 1959: **PPP** 212, 295.

***Thalamoporella*** new species **1** [similar to *T. biperforata,* but avicularia smaller and sibling zooids highly torqued (see Soule *et al.,* 1987, for terminology)]: **DR** NMB 15815, 16817, 16818, 16828, 16832–16836, 16838, 16839, 16842, 16844, 16995.

***Thalamoporella*** new species **2** [like *T. chubbi,* but avicularia slightly asymmetrical]: **DR** NMB 16818, 16833, 16836, 16838, 16914, 16917, 16923, 16927, 16932, 16935, 16938, 17184, 17265, 17268; Olsson 179.

***Thalamoporella*** new species **3** [small, pointed avicularia]: **DR** NMB 15900, 15903, 15904, 15906, 15907, 15910–15912, 15914, 15915, 16192, 16817, 16828, 16856, 16857, 16935; Olsson 179.

***Thalamoporella*** new species **4** [large zooids; rounded avicularia; sibling zooid slightly torqued]: **PPP** 35.

***Thalamoporella*** new species **5** [small, crescent-shaped avicularia; sibling zooid not torqued]: **PPP** 346.

***Thalamoporella*** new species **6** [rounded avicularia similar to zooids in size; sibling zooid moderately torqued]: **PPP** 370, 669, 708, 709, 720, 722, 723, 937.

***Vibracellina laxibasis*** Canu and Bassler, 1928: **PPP** 65, 66, 68, 69, 162, 178, 180, 205, 210–212, 295, 306, 308, 352, 362, 367, 368, 370, 631, 634, 635, 639, 640, 642, 644, 653, 663, 704, 709, 720, 722, 723, 738, 937, 943, 944, 948–950, 962, 963.

***Vibracellina*** aff. ***V. laxibasis*** Canu and Bassler, 1928: **DR** NMB 15805, 15815, 15829, 15832, 15833, 15835, 15836, 15900, 15901, 15934, 15962, 16103, 16192, 16817, 16818, 16832, 16833, 16835, 16865, 16936, 16938, 16942, 17023, 17175, 17184; TU 1294.

***Vincularia*** new species: **DR** NMB 16935, 16936, 16938, 16942, 17184, 17190, 17265, 17285, 17287–17290, 17327; Olsson 179.

## Suborder ASCOPHORINA Levinsen, 1909

***Adeonellopsis deformis*** (Canu and Bassler, 1919): **DR** NMB 15804, 15805, 15814, 15815, 15829, 15836–15838, 15840, 15854, 15860, 15873, 15874, 15878, 15881, 15882, 15896, 15900, 15901, 15906, 15912, 15934, 15962, 15964, 16167, 16186, 16191, 16192, 16802, 16817, 16818, 16828, 16832, 16833, 16835, 16860, 16865, 16910, 16913–16916, 16918, 16922, 16924, 16926–16930, 16932, 16975, 17268, 17269, 17273, 17307; Olsson 180; TU 1225, 1227A, 1294; USGS 8525, 8702.

***Adeonellopsis*** new species **1** [*A.* sp. of Cook, 1973, p. 252]: **DR** NMB 15838, 15840, 15842, 15846, 15849, 15860, 15863, 15865, 15871, 16910, 17175; TU 1227A, 1293.

***Adeonellopsis*** new species **2** [spiramen multiporous]: **DR** NMB 17273.

***Adeonellopsis*** new species **3**: **PPP** 334, 367, 368, 679, 683, 697, 704, 708–710, 720, 722, 723.

***Aimulosia palliolata*** (Canu and Bassler, 1928): **PPP** 47, 69, 86, 144, 146, 148, 156, 204, 308, 639, 642, 645, 670, 710, 720, 738, 944, 949, 950, 962, 963. **DR** NMB 15828, 15829, 15964, 16103.

***Arthropoma cecilii*** (Audoin, 1826): **PPP** 205.

new genus **B** new species **y** Scolaro, 1968: **PPP** 708, 709, 720, 722, 723. **DR** NMB 15823, 15828, 15835, 15838, 15842, 15846, 15849, 15851, 15853, 15854, 15860, 15863, 16811, 16856, 16910, 16935, 16936, 16938, 16942, 17023, 17184, 17190, 17265, 17278, 17283, 17284; Olsson 179; TU 1293; USGS 8702.

***Bellullopora bellula*** (Osburn, 1950): **PPP** 709, 950.

***Bracebridgia subsulcata*** (Smitt, 1873): **PPP** 68, 210, 212, 345, 631, 634, 635, 640, 642, 645, 663, 710, 712, 738, 940, 944, 948, 950, 962, 963.

***Buskea*** new species aff. ***B. dichotoma*** (Hincks, 1862): **PPP** 635, 639, 640, 642, 644, 653, 663, 943, 944, 948, 949, 950, 962, 963.

***Calyptooecia insidiosa*** Winston, 1984: **PPP** 639, 644, 949, 950, 962, 963. **DR** NMB 15838, 15840, 15846, 15849, 15853, 16865; USGS 8702.

***Celleporaria albirostris*** (Smitt, 1873): **PPP** 53, 68, 69, 71, 86, 144, 177, 210, 212, 346, 352, 361, 367, 631, 634, 635, 639, 640, 642, 644, 645, 653, 663, 712, 738, 832, 943, 944, 948–950, 962, 963.

***Celleporaria brunnea*** (Hincks, 1884): **PPP** 47, 64–66, 68, 86, 137, 148, 194, 198, 204–206, 210, 212, 214, 294, 295, 298, 308, 334, 335, 340, 341, 345, 346, 348–350, 362, 368, 391, 631, 634, 635, 639, 640, 642, 704, 709, 720, 722, 943, 944, 948–950, 962, 963. **DR** NMB 15804, 15815, 15832, 15833, 15837, 15846, 15849, 15853, 15865, 15871, 15934, 16103, 16935, 16936, 16938, 17175.

***Celleporaria magnifica*** (Osburn, 1914): **PPP** 148, 178, 180, 334, 367, 368, 634, 635, 639, 640, 642, 645, 704, 705, 709, 943, 950, 963. **DR** NMB 15842, 15846, 15849, 15860, 15878, 15881, 15901, 15911, 15912, 15914, 15915, 15962, 16167, 16192, 16817, 16818, 16828, 16832–16839, 16842, 16844, 16856, 16857, 16865, 16879, 16913–16918, 16924, 16926–16929, 16942, 16975, 16976, 16983, 16984, 16995, 17023, 17268, 17269, 17278, 17283; Olsson 179; TU 1294, 1379; USGS 8525, 8702.

***Celleporaria*** new species: **PPP** 352.

***Characodoma contractum*** (Waters, 1899): **PPP** 47, 60, 65, 68, 69, 86, 137, 144, 146, 148, 156, 162, 178, 180, 193, 194, 196, 204–207, 307, 311, 326, 340, 346, 350, 352, 354, 355, 357, 367, 368, 422, 631, 634, 635, 639, 640, 642, 645, 709, 710, 720, 722, 723, 943, 944, 948–950, 962, 963.

***Cigclisula porosa*** (Canu and Bassler, 1919): **PPP** 65, 68, 69, 74, 205, 206, 210, 294, 298, 307, 308, 340, 341, 345, 346, 348, 365, 391, 631, 634, 635, 639, 640, 642, 645, 663, 670, 679, 697, 704, 708, 709, 720, 722, 723, 932, 944, 949, 950, 962, 963. **DR** NMB 15805, 15842, 15846, 15851, 15854, 15860, 15863–15865, 15871, 15934, 16828, 16834–16836, 16842, 16844, 16910, 16913, 16915, 16916, 16918, 16924, 16926–16928, 16932, 16935, 16938, 16942, 17184, 17190, 17265, 17268, 17269, 17283, 17285–17290, 17327; Olsson 179; TU 1294.

***Coleopora*** aff. ***C. americana*** Osburn, 1940: **PPP** 644, 949, 962.

***Coleopora granulosa*** Canu and Bassler, 1928: **PPP** 205. **DR** NMB 15823, 15828, 15829, 15832, 15833, 15838, 15840, 15849, 15851, 15853, 15962, 16811, 16818, 17023, 17175.

***Crepidacantha longiseta*** Canu and Bassler, 1928: **PPP** 639, 949, 950.

***Crepidacantha poissonii*** (Audouin, 1826): **PPP** 60, 67, 86, 144, 949.

***Cycloperiella rubra*** Canu and Bassler, 1923: **PPP** 47, 65, 86, 144, 162, 340, 350, 352, 722, 723.

***Cycloperiella*** new species: **PPP** 65, 205, 294, 295, 298, 306, 307, 334, 335, 346, 348, 350, 352.

***Ditaxipora*** new species **1**: **PPP** 65, 349, 355, 708, 711, 720, 722, 723. **DR** NMB 15823, 15838, 15849, 15900, 15911, 15912, 15914, 15915, 16817, 16818, 16828, 16833, 16836, 16838, 16844, 16856, 16913, 16918, 16929, 17023; USGS 8525.

***Ditaxipora*** new species **2**: **DR** NMB 15837, 15846, 15851, 15853.

***Drepanophora tuberculatum*** (Osburn, 1914): **PPP** 631. **DR** NMB 15842, 15846, 15849, 15853, 16811, 16828, 16832, 16856, 16865, 16915, 16916, 16926, 16928, 16929; USGS 8702.

***Escharella***? species: **PPP** 210.

***Escharina pesanseris*** (Smitt, 1873): **PPP** 639, 663, 709, 738, 948–950. **DR** NMB 15846, 15853, 15860, 17023.

***Escharina porosa*** (Smitt, 1873): **PPP** 634, 635, 639, 640, 642, 944, 948–950, 963. **DR** NMB 15838, 15851, 15853, 15962, 16811, 16855, 16856.

***Escharoides costifer*** (Osburn, 1914): **PPP** 949.

***Escharoides*** new species [like *E. costifer,* but with avicularia curved and directed distolaterally]: **DR** NMB 15853, 15865, 16818.

***Exechonella*** cf. ***E. antillea*** (Osburn, 1927): **DR** NMB 15838, 15846.

***Fedora*** aff. ***F. nodosa*** Silén, 1947: **DR** NMB 15804, 15805, 15814, 15815, 15829, 15833, 15835, 15836, 15863, 15934, 15962, 15964, 16828, 17175; Olsson 180; TU 1293, 1294.

***Gemellipora*** new species **1** [small zooids]: **DR** NMB 15823, 15832, 15833, 17023.

***Gemellipora*** new species **2** [large zooids]: **DR** NMB 15823, 15832, 15833, 17023.

***Gemelliporella glabra*** Smitt, 1873: **PPP** 361, 710, 712.

***Gemelliporella punctata*** Canu and Bassler, 1919: **PPP** 35, 68, 69, 72, 162, 180, 183, 210–212, 214, 340, 365, 367, 368, 370, 390, 422, 645, 653, 663, 668, 679, 683, 689, 932, 935, 937, 940. **DR** NMB 15804, 15814, 15815, 15835, 15836, 15842, 15849, 15878, 15881, 15882, 15890, 15900, 15912, 15962, 16167, 16817, 16818, 16828, 16832, 16833, 16835, 16836, 16837, 16839, 16842, 16844, 16857, 16860, 16913, 16915, 16916, 16918, 16924, 16926, 16927, 16928, 16929, 16995, 17023, 17175, 17268, 17269; TU 1225, 1293, 1379; USGS 8525, 8702.

***Gemelliporella***? new species [colony adeoniform]: **PPP** 365, 634, 640, 642, 644, 645, 663, 704, 720, 722, 935, 943, 944, 948–950, 962, 963. **DR** NMB 15804, 15814, 15815, 15823, 15962, 16103.

***Gemelliporidra magniporosa*** (Canu and Bassler, 1923): **PPP** 47, 639, 949.

***Gemelliporidra multilamellosa*** (Canu and Bassler, 1923): **PPP** 55, 65, 631, 634, 635, 639, 640, 642, 644, 645, 663, 709, 710, 712, 943, 944, 948–950, 962, 963.

***Gemelliporidra***? species: **DR** NMB 15815, 15846, 15849, 15851, 15853, 15854, 15878, 15911, 15962, 15964, 16811, 16817, 16818, 16855, 16856, 16865, 17268, 17278.

***Gephyrophora*** cf. ***G. rubra*** Osburn, 1940: **DR** NMB 16834.

***Gigantopora fenestrata*** (Smitt, 1873): **PPP** 639, 644, 710, 949, 963. **DR** NMB 15851, 17023.

***Hippaliosina rostrigera*** (Smitt, 1873): **PPP** 65, 68, 69, 86, 205, 210, 212, 295, 298, 326, 631, 634, 635, 639, 640, 642, 645, 653, 709, 720, 722, 723, 944, 948–950, 962, 963.

***Hippaliosina*** new species: **DR** NMB 16855, 16915.

***Hippomenella***? ***fissurata*** (Canu and Bassler, 1928): **PPP** 65, 298, 634, 635, 639, 640, 645, 653, 943, 944, 948, 950, 962, 963.

***Hippomenella***? aff. ***H.***? ***fissurata*** (Canu and Bassler, 1928): **DR** NMB 16834, 16835, 16838, 16839, 16995.

***Hippopetraliella*** cf. ***H. marginata*** (Canu and Bassler, 1928): **DR** NMB 15842, 15846, 15854, 16817, 16828, 16832, 16833, 16836–16839, 16842, 16856, 15849.

***Hippopleurifera mucronata*** (Smitt, 1873): **PPP** 47, 86, 144, 146, 148, 352.

***Hippopleurifera*** new species **1**: **DR** NMB 16818, 16828, 16833.

***Hippopleurifera*** new species **2**: **PPP** 710, 949.

***Hippopodina*** cf. ***H. bernardi*** Lagaaij, 1963: **DR** NMB 15911, 15914, 16835, 16836.

***Hippopodina feegeensis*** (Busk, 1884): **PPP** 635.

***Hippopodina*** aff. ***H. feegeensis*** (Busk, 1884): **DR** NMB 15849, 15851, 15853, 15915, 16811, 16832, 16935, 16936.

***Hippoporella costulata*** Canu and Bassler, 1923: **PPP** 68, 69, 86, 144, 156, 210, 212, 631, 634, 635, 639, 645, 704, 709, 710, 720, 738, 944, 950, 962, 963.

***Hippoporella gorgonensis*** Hastings, 1930: **PPP** 47, 64–66, 68, 86, 89, 137, 144, 146, 148, 156, 162, 193–196, 198, 204–208, 294, 295, 307, 311, 312, 326, 345, 350, 352, 355, 379, 631, 639, 640, 644, 653, 670, 709, 937, 943, 949, 950, 962, 963, 1171. **DR** NMB 15809, 15814, 15836, 15837, 15842, 15846, 15849, 15851, 15853, 15854, 15860, 15863, 15865, 15881, 15900, 15964, 16802, 16811, 16833–16836, 16839, 16844, 16855–16857, 16860, 16865, 16914, 16995, 17268; USGS 8702.

***Hippoporella*** aff. ***H. rimata*** Osburn, 1952: **PPP** 47, 148, 205, 206, 307, 352, 962.

***Hippoporidra edax*** (Busk, 1859): **PPP** 10, 47, 65, 66, 86, 137, 144, 146, 148, 156, 180, 188, 212, 354, 639, 697, 704, 709, 720, 722, 723, 832, 950, 1142.

***Hippoporina aculeata*** (Canu and Bassler, 1928): **PPP** 65, 68, 69, 144, 148, 156, 162, 204, 206, 210, 291, 326, 340, 345, 350, 352, 355, 631, 640, 642, 645, 704, 708, 710, 738, 944.

***Hippoporina*** new species **1**: **PPP** 60, 294, 298.

***Hippoporina*** new species **2**: **PPP** 66, 86, 137, 146.

***Hippoporina*** new species **3**: **PPP** 86, 137, 144.

***Hippoporina***? species: **DR** NMB 15840, 15934, 16828, 17175; Olsson 179.

***Jaculina*** species **x** (Scolaro, 1968): **DR** NMB 16935, 17184, 17285–17289, Olsson 179.

***Lagenicella marginata*** (Canu and Bassler, 1930): **PPP** 635, 642, 644, 738, 949, 962.

***Lagenicella*** aff. ***L. mexicana*** (Osburn, 1952): **PPP** 68, 86, 137, 144, 146, 156, 211, 312, 367, 634, 781, 835, 950.

***Lagenicella*** new species: **PPP** 86, 144, 146, 210, 645, 949, 963.

***Lagenicella*** species: **DR** NMB 15832, 16817, 16818, 16828, 16833, 16836, 16841, 16842, 16928, 17269.

***Lagenipora*** species: **PPP** 640, 712.

***Mamillopora cavernulosa*** Canu and Bassler, 1928: **PPP** 55, 57, 65, 197, 198, 294, 295, 298, 306–308, 312, 334, 335, 340, 345, 350, 352, 354, 357, 358, 635, 639, 640, 653, 663, 688, 689, 691, 695, 704, 709, 710, 720, 722, 723, 738, 937, 940, 944, 950.

***Mamillopora tuberosa*** Canu and Bassler, 1918: **PPP** 10, 47, 55, 57, 60, 63–69, 71, 72, 74, 86, 137, 144, 146, 148, 156, 162, 178, 180, 183, 193–196, 198, 203–208, 210, 214, 294, 306, 307, 311, 312, 334, 335, 341, 345, 346, 348, 350, 352, 354, 355, 357, 362, 365, 367, 368, 370, 379, 419, 422, 423, 425, 426, 631, 634, 635, 639, 640, 642, 644, 645, 653, 668–673, 675–679, 683, 685, 689, 691, 697, 704, 705, 708, 709, 720, 722, 723, 832, 833, 908, 931–933, 935, 939, 943, 944, 948, 962, 963, 1145, 1171. **DR** NMB 15805, 15814, 15815, 15833, 15835, 15836, 15840, 15846, 15860, 15863–15865, 15869, 15871, 15873, 15874, 15876, 15878, 15881, 15882, 15890, 15895–15897, 15900, 15901, 15903, 15904, 15906, 15907, 15910–15912, 15914, 15915, 15934, 15942, 15962, 15964, 15965, 15968, 15969, 15974, 16167, 16186, 16191, 16192, 16802, 16810, 16817, 16818, 16824, 16827, 16828, 16832–16839, 16842, 16844, 16854, 16856, 16857, 16860, 16865, 16910, 16912–16915, 16917, 16918, 16922–16924, 16926, 16927, 16929, 16930, 16932, 16935, 16938, 16961, 16970, 16971, 16973, 16975, 16978, 16985, 16995, 17005, 17175, 17184 17268, 17269, 17283, 17286–17290, 17322, 17327; Olsson 179, 180, TU 1225, TU 1293, 1294; USGS 8525, 8702.

***Mamillopora*** new species **1** [large, pointed avicularia on basal side]: **PPP** 53, 171, 175, 177, 178, 180, 212, 358, 361, 362, 365, 367, 368, 370, 631.

***Mamillopora*** new species **2** [tiny, conical colonies]: **PPP** 61, 62, 63, 187, 200, 201, 308, 362.

***Margaretta buski*** Harmer, 1957: **PPP** 35, 65, 68, 86, 144, 146, 156, 210, 211, 350, 367, 631, 634, 635, 640, 642, 644, 645, 663, 679, 708, 709, 710, 712, 720, 738, 932, 939, 940, 943, 944, 948, 949, 950, 962, 963.

***Margaretta*** new species **1**: **DR** NMB 15804, 15814, 15815, 15837, 15838, 15840, 15842, 15846, 15849, 15851, 15853, 15854, 15860, 15863, 15864, 15871, 15878, 15881, 15882, 15900, 15914, 15915, 15934, 15962, 15964, 16167, 16811, 16817, 16818, 16828, 16832, 16833, 16835–16838, 16842, 16856, 16857, 16910, 16913, 16916, 16918, 16926, 16927, 16929, 16936, 16938, 16942, 17023, 17190, 17265, 17268; Olsson 179; USGS 8702.

***Margaretta*** new species **2**: **DR** NMB 17184, 17290.

***Membraniporella***? species: **PPP** 634, 670.

***Metrarabdotos auriculatum*** Canu and Bassler, 1923: **PPP** 68, 210, 211, 212, 671, 689, 691. **DR** NMB 15876, 15878, 15881, 15882, 16167, 16186, 16817, 16818, 16824, 16828, 16836, 16837, 16839, 16842–16844, 16846, 16852, 16857, 16858, 16959, 16961, 16962, 16970–16972, 16984, 16986, 16988, 16989, 16993, 16995, 17005, 17012, 17019, 17026.

***Metrarabdotos colligatum*** Canu and Bassler, 1919: **PPP** 191, 423. **DR** NMB 15869, 15876, 15878, 15881, 15890, 15895–15897, 15900, 15904, 15906, 15907, 15910–15912, 15914, 15915, 16167, 16191, 16802, 16844, 16852, 16857, 16910, 16912–16918, 16922–16924, 16926–16930, 16932, 17175, 17268, 17269; TU 1293, 1294, 1379; USGS 8525, 8702.

***Metrarabdotos lacrymosum*** Canu and Bassler, 1919: **PPP** 212, 362. **DR** NMB 15804, 15814, 15815, 15833, 15835, 15846, 15849, 15854, 15860, 15863–15865, 15873, 15874, 15878, 15881, 15882, 15890, 15911–15913, 15915, 15934, 15962, 15964, 16167, 16802, 16817, 16818, 16824, 16828, 16832–16839, 16842, 16844, 16858, 16930, 16984, 16988, 16989, 16995, 17286; TU 1225.

***Metrarabdotos pacificum*** (Osburn, 1952): **PPP** 66, 86, 144, 146, 156, 257, 271.

***Metrarabdotos tenue*** (Busk, 1884): **DR** NMB 17268.

***Metrarabdotos unguiculatum*** Canu and Bassler, 1928: **PPP** 211, 723. **DR** NMB 16833.

***Metrarabdotos*** new species **1** Cheetham, 1986: **DR** NMB 17265, 17284, 17286–17290; Olsson 179.

***Metrarabdotos*** new species **2** Cheetham, 1986: **DR** NMB 16935, 16936, 16938, 16942, 17184, 17265; Olsson 179.

***Metrarabdotos*** new species **3** Cheetham, 1986: **DR** NMB 15837, 15838, 15840, 15842, 15846, 15860, 15863, 15864, 15900, 16191, 16910, 17175; TU 1293; USGS 8702.

***Metrarabdotos*** new species **4** Cheetham, 1986: **DR** NMB 15804, 15814, 15835, 15836, 15838, 15840, 15842, 15846, 15849, 15860, 15863–15865, 15869, 15871, 15934, 15962, 16810, 16811, 16833; Olsson 180; TU 1225, 1293.

***Metrarabdotos*** new species **5** Cheetham, 1986: **DR** NMB 15900, 15901, 15903, 15906, 15910, 15911, 16839, 16844, 16986, 16988, 16989, 16993, 16995.

***Metrarabdotos*** new species **6** Cheetham, 1986: **DR** NMB 15878, 15881, 15882, 15904, 15906, 16191.

***Metrarabdotos*** new species **7** Cheetham, 1986: **DR** NMB 15804, 15805, 15814, 15815, 15835, 15836, 15842, 15849, 15934, 16910, 17175; Olsson 180; TU 1293.

***Metrarabdotos*** new species **8** Cheetham, 1986: **PPP** 35, 60, 68, 210, 211, 352, 653. **DR** NMB 15860, 15863, 15864, 15869, 15873, 16810; USGS 8702.

***Metrarabdotos*** new species **9** Cheetham, 1986: **DR** NMB 16817, 16824, 16828, 16832–16834, 16838, 16879, 16959, 16961, 16970–16973, 16975, 16976, 16978, 17005, 17268; USGS 8702.

***Metrarabdotos*** new species **10** Cheetham, 1986: **PPP** 214, 335, 348, 349, 352, 663, 679, 708, 709, 720, 722, 723. **DR** NMB 15804, 15815, 15934, 15962, 16817, 16818, 16824, 16828, 16832–16835, 16837, 16838, 16842, 16844, 16961, 16976, 16983, 16984; USGS 8702.

***Microporella*** cf. ***M. ciliata*** (Pallas, 1766): **DR** NMB 15851, 15853, 17023.

***Microporella normani*** Canu and Bassler, 1928: **PPP** 86, 144, 148, 156, 162, 773, 832, 1152.

***Microporella umbracula*** (Audouin, 1826): **PPP** 47, 65, 86, 144, 146, 148, 180, 352, 354, 367, 391, 635, 639, 640, 642, 653, 663, 709, 720, 723, 943, 944, 948, 950, 962, 963.

***Odontoporella adpressa*** (Busk, 1854): **PPP** 47, 66, 86, 144, 146, 148, 156, 832, 949, 950.

***Parasmittina*** aff. ***P. areolata*** (Canu and Bassler, 1927): **PPP** 65, 204, 206, 210, 294, 307, 326, 334, 335, 634, 639. **DR** NMB 16828, 16832–16834, 16865, 16913–16918, 16922, 16926–16929, 16932, 16935, 17269; TU 1294; USGS 8525.

***Parasmittina crosslandi*** (Hastings, 1930): **PPP** 47, 68, 86, 144, 146, 156, 196, 206, 257, 271, 292, 307, 350, 352.

***Parasmittina fraseri*** Osburn, 1952: **PPP** 47, 60, 66, 86, 144, 146, 148, 156, 205, 271, 291, 292.

***Parasmittina hastingsae*** Soule and Soule, 1973: **PPP** 68, 69, 963.

***Parasmittina*** aff. ***P. murarmata*** (Kirkpatrick, 1888): **PPP** 670, 671, 708, 937, 963.

***Parasmittina parsevaliformis*** Soule and Soule, 1973: **PPP** 65, 137, 205, 210, 212, 222, 294, 298, 308, 340, 631, 634, 635, 639, 642, 644, 645, 704, 722, 943, 944, 948, 950, 962, 963. **DR** NMB 15934, 16817, 16818, 16828, 16832–16834, 16836, 16838, 16842, 16865, 17268; Olsson 179.

***Parasmittina spathulata*** (Smitt, 1873): **PPP** 222, 352, 640, 642, 644, 710, 943, 944, 949, 950, 962, 963. **DR** NMB 15815, 15849, 15851, 15878, 15881, 15882, 15912, 15914, 16167, 16811, 16836, 16837.

***Parasmittina*** new species **1**: **PPP** 65, 222, 634, 635, 644, 944. **DR** NMB 15881, 15915, 16828, 16833, 16834, 16836–16839, 16856, 16916, 16995; USGS 8702.

***Parasmittina*** new species **2**: **DR** NMB 16856, 16913, 16915–16918, 16922, 16926–16929, 17269; TU 1294; USGS 8525.

***Parasmittina*** new species **3**: **PPP** 640, 642, 645, 709, 710, 720, 944, 949, 950, 962. **DR** NMB 15849, 16818, 17265.

***Parasmittina*** new species **4**: **DR** NMB 16913, 16916, 16922, 16928; TU 1294; USGS 8525.

***Parasmittina*** new species **5**: **DR** NMB 15842.

***Parasmittina*** new species **6**: **DR** NMB 15851, 15853.

***Parasmittina*** new species **7**: **PPP** 631.

***Parasmittina*** new species **8**: **PPP** 86, 148, 205.

***Parkermavella punctigera*** (MacGillivray, 1883): **PPP** 631, 949.

***Pasythea tulipifera*** (Ellis and Solander, 1786): **PPP** 64, 65.

***Pasythea*** new species: **DR** NMB 15900, 15901, 15906, 15907, 15934, 15962, 16833, 16835, 16836, 16838, 16916, 16926, 16928, 16935, 16936, 16938, 16995, 17184, 17190, 17265, 17307, 17327; Olsson 179; TU 1294; USGS 8525, 8702.

***Petraliella bisinuata*** (Smitt, 1873): **PPP** 68, 69, 210–212, 361, 362, 631, 634, 635, 639, 640, 642, 645, 663, 704, 712, 738, 943, 944, 950, 963.

***Pleurocodonellina*** species: **PPP** 68, 210.

***Puellina innominata*** (Couch, 1844): **PPP** 86, 144, 146, 709.

***Puellina radiata*** (Moll, 1803): **PPP** 148, 205, 210, 348, 352, 631, 640, 670, 738, 944, 949, 950, 963.

***Puellina*** new species aff. ***P. radiata*** (Moll, 1803): **PPP** 69, 639, 642, 645, 653, 708–710, 723, 943, 949, 950, 962, 963.

***Puellina*** species: **DR** NMB 15823, 15853, 16811, 16860, 17023.

***Reptadeonella bipartita*** (Canu and Bassler, 1928): **PPP** 47, 65–69, 86, 144, 146, 148, 156, 205, 271, 352, 670, 937. **DR** NMB 15842, 15864, 16855, 16856; TU 1227A; USGS 8702.

***Reptadeonella hastingsae*** Cheetham and Sandberg, 1964: **DR** NMB 15878, 16167, 16856, 16865,16942.

***Reptadeonella tubulifera*** (Canu and Bassler, 1930): **PPP** 47, 66, 86, 144, 146, 148, 156, 201, 214. **DR** NMB 17023.

***Reptadeonella*** new species [similar to *R. joloensis* (Bassler, 1935) and other Pacific species]: **DR** NMB 15823, 15828, 15829, 15840, 15849, 15851, 15853, 15854, 16811.

***Reteporellina evelinae*** Marcus, 1958: **PPP** 35, 68, 69, 86, 144, 156, 180, 183, 210–212, 367, 368, 631, 634, 635, 639, 640, 642, 644, 645, 653, 663, 704, 708, 709, 712, 720, 722, 723, 738, 943, 944, 948–950, 962, 963. **DR** NMB 15823, 15828, 15832, 15833, 15837, 15853, 16856, 17023.

***Rhynchozoon*** aff. ***R. phyrnoglossum*** Marcus, 1932: **PPP** 148.

***Rhynchozoon rostratum*** (Busk, 1856): **PPP** 47, 63, 65, 66, 86, 144, 206, 207, 294, 352, 355, 422, 634, 639, 642, 644, 943, 944, 949, 950, 962.

***Rhynchozoon verruculatum*** (Smitt, 1873): **PPP** 146, 148, 156.

***Rhynchozoon*** species [at least three species]: **DR** NMB 15842, 15869, 15871, 15878, 15881, 15882, 15906, 15911, 15912, 15914, 15915, 15962, 16167, 16186, 16810, 16817, 16818, 16828, 16832–16836, 16839, 16842, 16844, 16855–16857, 16913–16916, 16918, 16922, 16926–16930, 16935, 16936, 16938, 16942, 17184, 17265, 17269, 17288–17290; Olsson 179; TU 1294, 1379.

***Savignyella*** species: **DR** NMB 15823, 15837, 16817, 17023, 17184; Olsson 179.

**savignyellid**? species [new genus with biserial branches]: **DR** NMB 17184; Olsson 179.

***Schedocleidochasma cleidostoma*** (Smitt, 1873): **PPP** 47, 66, 68, 69, 86, 144, 162, 180, 210, 212, 294, 295, 298, 308, 334, 335, 340, 341, 345, 348, 350, 361, 362, 367, 368, 370, 634, 635, 639, 640, 642, 644, 653, 663, 668, 669, 671, 704, 709, 710, 720, 722, 723, 943, 944, 948–950, 963.

***Schedocleidochasma porcellanum*** (Busk, 1860): **PPP** 86, 146, 148, 156. **DR** NMB 15833, 15846, 15849, 15851, 15853, 15854, 15863, 15882, 15911, 15912, 15914, 15915, 15934, 16811, 16817, 16818, 16832–16836, 16842, 16855, 16856, 16865, 16913, 16915, 16916, 16918, 16922, 16924, 16926–16930, 16936, 16938, 17190, 17265, 17269; TU 1294; USGS 8525.

***Schedocleidochasma*** new species **1**: **PPP** 64, 65, 198, 308, 340, 341, 345, 350, 352, 634.

***Schedocleidochasma*** new species **2**: **PPP** 937, 949.

***Schedocleidochasma*** new species **3**: **PPP** 64–66, 68, 69, 178, 180, 204, 205, 210, 212, 214, 294, 295, 298, 306–308, 312, 326, 334, 335, 340, 341, 345, 348–350, 352, 354, 358, 367, 368, 370, 631, 634, 635, 639, 640, 642, 663, 668, 670, 672, 710, 738, 944, 948, 950, 962, 963.

***Schizoporella cornuta*** (Gabb and Horn, 1862): **PPP** 60, 63–69, 86, 144, 146, 148, 156, 162, 188, 194, 196, 198, 204, 206, 212, 294, 295, 298, 308, 311, 312, 326, 334, 346, 350, 352, 355, 635, 639, 640, 642, 705, 709, 722, 723, 835, 944, 949, 950, 963, 1171.

***Schizoporella floridana*** Osburn, 1914: **PPP** 419, 422.

***Schizoporella magniporosa*** (Canu and Bassler, 1923): **PPP** 334, 368, 679, 691, 704, 708, 709, 720, 722, 723. **DR** NMB 15804, 15805, 15814, 15815, 15829, 15835–15838, 15840, 15842, 15846, 15849, 15853, 15860, 15863–15865, 15869, 15878, 15881, 15882, 15900, 15911, 15934, 15962, 15964, 16103, 16167, 16186, 16810, 16811, 16817, 16818, 16828, 16832, 16833–16835, 16842, 16865, 16910, 16913, 16915, 16916, 16918, 16924, 16926–16930, 17023, 17175, 17268, 17269; TU 1293, 1379; USGS 8525, 8702.

***Semihaswellia sinuosa*** (Canu and Bassler, 1928): **PPP** 68, 210, 631, 644, 645, 653, 663, 738, 943, 944, 948–950, 962, 963. **DR** NMB 15804, 15814, 15815, 15823, 15828, 15837, 15838, 15842, 15846, 15849, 15854, 15860, 15863–15865, 15871, 15934, 15962, 15964, 16811, 16910, 17023, 17175; USGS 8702.

***Smittina***? new species **1**: **PPP** 823, 833.

***Smittina***? new species **2**: **PPP** 944, 963.

***Smittoidea maleposita*** (Canu and Bassler, 1923): **PPP** 86, 137, 144, 146, 156, 180, 335, 350, 367, 368, 709. **DR** NMB 16938; Olsson 179.

***Smittoidea pacifica*** Soule and Soule, 1973: **PPP** 653, 949.

***Smittoidea prolifica*** Osburn, 1952: **PPP** 86.

***Stylopoma informatum*** (Lonsdale, 1845): **DR** TU 1294; USGS 8525.

***Stylopoma minutum*** (Canu and Bassler, 1923): **PPP** 55, 65, 66, 67, 68, 69, 144, 146, 148, 205, 206, 307, 334, 335, 340, 346, 350, 352, 355, 464, 704, 709, 937. **DR** NMB 15882, 16837, 16916.

***Stylopoma projectum*** (Canu and Bassler, 1923): **PPP** 631, 634, 712, 722, 723.

***Stylopoma spongites*** (Pallas, 1766): **PPP** 210, 222, 368, 464, 639, 645, 709, 944, 948, 962, 963. **DR** NMB 15912, 15914, 15915, 16817, 16818, 16828, 16832, 16834–16837, 16839, 16844, 16856, 16857, 16913, 16914, 16916, 16928, 16929, 16932, 16995, 17268, 17269; TU 1294; USGS 8525.

***Stylopoma*** new species **3** Jackson and Cheetham, 1994: **PPP** 631, 634, 635, 640, 712, 720, 943, 949, 950.

***Stylopoma*** new species **4** Jackson and Cheetham, 1994: **DR** NMB 15838, 15851, 15962; Olsson 180.

***Stylopoma*** new species **5** Jackson and Cheetham, 1994: **DR** NMB 16928, 16929.

***Stylopoma*** new species **6** Jackson and Cheetham, 1994: **DR** NMB 16832, 16833, 16913, 16916, 16924, 16928, 17265, 17269; Olsson 179.

***Stylopoma*** new species **7** Jackson and Cheetham, 1994: **DR** NMB 16811, 16833, 16835, 16838, 16842, 16865, 17268.

***Stylopoma*** new species **11** Jackson and Cheetham, 1994: **PPP** 367, 634, 712, 943, 944, 949, 950, 962, 963.

***Stylopoma*** new species **13** Jackson and Cheetham, 1994: **PPP** 294, 295, 298, 710, 722. **DR** NMB 15869, 16928.

***Stylopoma*** new species **14** Jackson and Cheetham, 1994: **PPP** 639, 640. **DR** NMB 15863, 16910.

***Tetraplaria dichotoma*** (Osburn, 1914): **PPP** 180, 631, 720. **DR** NMB 15805, 15823, 15827, 15835, 15838, 15846, 15849, 15851, 15853, 15860, 15964, 16811, 16828, 16833, 16856, 17268.

***Trematooecia aviculifera*** (Canu and Bassler, 1923): **PPP** 55, 210, 634, 710, 738, 949, 962, 963. **DR** NMB 15849, 15962, 16916, 16928, 16929; USGS 8702.

***Trematooecia*** cf. ***T. hexagonalis*** (Canu and Bassler, 1930): **DR** NMB 15805, 15814, 15838, 15854, 16811, 17023; USGS 8702.

***Trematooecia turrita*** (Smitt, 1873): **PPP** 55, 64, 65, 86, 146, 148, 156, 645, 720, 944, 949, 950, 963. **DR** NMB 15804, 15814, 15815, 15838, 15840, 15849, 15962, 16828, 16860, 16865.

***Trematooecia vaughani*** (Canu and Bassler, 1919): **DR** NMB 15836, 15838, 15840, 15846, 15878, 15882, 15890, 16167, 16817, 16818, 16828, 16832–16839, 16842, 16844, 16855, 16856, 16916, 16928, 16929, 16984, 16995; USGS 8702.

***Tremogasterina mucronata*** (Smitt, 1873): **PPP** 68, 69, 198, 210, 211, 294, 295, 298, 308, 334, 335, 340, 341, 345, 348, 368, 631, 634, 635, 639, 640, 642, 644, 645, 653, 685, 704, 709, 710, 720, 722, 723, 738, 932, 943, 944, 948–950, 962, 963. **DR** NMB 15804, 15814, 15815, 15836–15838, 15842, 15846, 15849, 15851, 15853, 15854, 15860, 15863, 15864, 15876, 15878, 15881, 15882, 15890, 15911, 15912, 15914, 15915, 15934, 15962, 15964, 16167, 16811, 16817, 16818, 16828, 16832, 16833–16839, 16842, 16844, 16857, 16865, 16910, 16917, 16918, 16922–16924, 16926–16929, 16935, 16936, 16938, 16942, 16983, 16988, 16989, 16993, 16995, 17023, 17175, 17184, 17190, 17265, 17268, 17269, 17288, 17289, 17290, 17327; Olsson 179; TU 1293.

***Tremoschizodina lata*** (Smitt, 1873): **PPP** 631, 738.

***Triporula stellata*** (Smitt, 1873): **PPP** 137, 631, 639, 640, 663, 943, 950, 963.

***Trypostega venusta*** (Norman, 1864): **PPP** 34, 47, 60, 66, 69, 86, 144, 146, 148, 150, 156, 348, 391, 634, 709, 720, 722, 723.

***Trypostega*** species: **DR** NMB 16817, 16836.

***Turbicellepora*** species: **PPP** 47, 65, 66, 86, 144, 146, 148, 156, 177, 178, 205, 210, 212, 295, 298, 306, 308, 334, 352, 422, 631, 639, 640, 642, 663, 670, 671, 672, 704, 705, 709, 720, 722, 723, 738, 944, 948, 962, 963.

***Vittaticella*** species: **DR** NMB 16833, 16935, 16938, 17184; Olsson 179; USGS 8525.

***Watersipora subovoidea*** (d'Orbigny, 1852): **PPP** 148.

## CHAPTER 9

# DIVERSITY AND ASSEMBLAGES OF NEOGENE CARIBBEAN MOLLUSCA OF LOWER CENTRAL AMERICA

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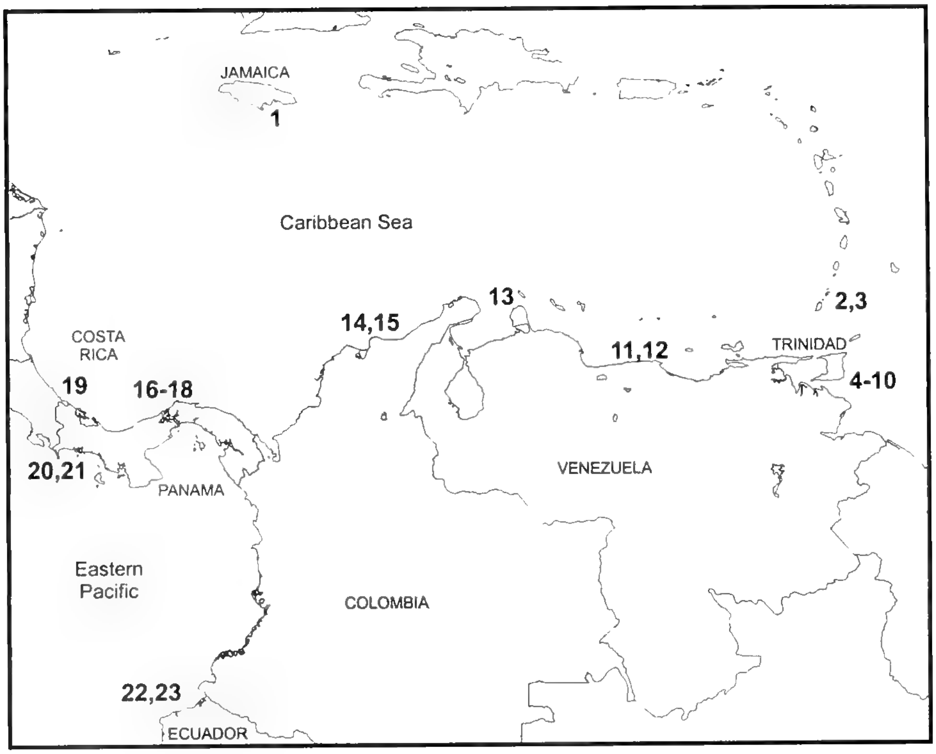
## INTRODUCTION

Our goal is to document and understand paleobiological patterns and trends for tropical American mollusks in marine coastal environments in relation to the rise of the lower Central American isthmus and global climate change. The time frame is the Neogene defined by the new Cenozoic chronology as the last 23.7 million years (Berggren *et al.*, 1995a, 1995b) when most modern clades of mollusks diversified. To this end, we have attempted to sample the cells of a 3-dimensional matrix whose axes are gradients in time, spatial scale and environment. Recent molluscan faunas differ greatly among geographic regions and environments (Sanders, 1968; Jackson, 1972, 1974; Rex, 1981; Roy *et al.*, 1996, 1998), and the same was true in the past (Valentine and Jablonski, 1993; Koch 1995,1996; Roy *et al.*, 1995). Therefore, it is necessary in paleobiological surveys to sample many geographic locations and environments throughout the entire time interval in question, and to know something about the environments of deposition of each sample. Otherwise, it is impossible to establish whether differences among faunas of different ages represent temporal trends or are artifacts of sampling different regions or environments over time. In addition, it is necessary to sample rigorously and consistently every cell of the 3-dimensional matrix so that observed differences between ages, places and environments are not artifacts of differential sampling effort (Koch 1987, 1995, 1996; Koch and Morgan, 1988; Sepkoski and Koch, 1995). For all these reasons, hypotheses of major evolutionary events (Petuch, 1995) or the division of paleobiogeographic provinces (Petuch, 1988) based on a few new taxa are only speculation.

Neogene mollusks of tropical America have been studied extensively during the past century, with detailed monographic descriptions of faunas ranging from Trinidad to Ecuador in the south, to Florida and Chiapas in the north. Some of these published faunas are very diverse (Text-fig. 1, Table 1), with the record held by Woodring's (1925–1928) systematic monographs of the Late Pliocene Bowden Formation in Jamaica with 347 genera or subgenera and 610 species. However, most of the other paleontological collections were made by petroleum geologists for the purpose of



Text-figure 1.—Location of Neogene molluscan faunas listed in Table 1.

Table 1.—Numbers of genera and subgenera reported in the major monographs of Neogene and Quaternary molluscan faunas of southern tropical America from Trinidad to Costa Rica to Ecuador. Taxa were counted as listed by the authors with no attempt to reconcile taxonomic usage over the years. G/SG = genera and subgenera. Blank spaces for scaphopods mean that they were not described rather than absent.

| | Bivalves | | Scaphopods | | Gastropods | | Total mollusks | |
|---|---|---|---|---|---|---|---|---|
| Formation or fauna | G/SG | Species | G/SG | Species | G/SG | Species | G/SG | Species |
| 1. Bowden, Jamaica | 117 | 187 | 10 | 20 | 220 | 406 | 347 | 610 |
| 2. Grand Bay, Carriacou | 18 | 20 | 1 | 2 | 70 | 87 | 89 | 109 |
| 3. Belmont, Carriacou | 8 | 8 | 1 | 1 | 34 | 44 | 43 | 53 |
| 4. Brasso, Trinidad | 21 | 28 | | | 18 | 23 | 39 | 51 |
| 5. Manzanilla, Trinidad | 24 | 35 | | | 16 | 22 | 40 | 57 |
| 6. Springvale, Trinidad | 25 | 35 | | | 31 | 47 | 56 | 92 |
| 7. Springvale, Trinidad | 46 | 56 | 2 | 3 | 61 | 95 | 119 | 154 |
| 8. Melajo, Trinidad | 45 | 57 | 1 | 1 | 88 | 110 | 134 | 168 |
| 9. Coubaril, Trinidad | 45 | 55 | 1 | 1 | 37 | 40 | 83 | 96 |
| 10. Matura, Trinidad | 47 | 58 | 3 | 3 | 82 | 92 | 132 | 160 |
| 11. Mare, Venezuela | 65 | 82 | | | 99 | 144 | 164 | 226 |
| 12. Malquetia, Venezuela | 42 | 53 | | | 65 | 82 | 107 | 135 |
| 13. Cantaure, Venezuela | 37 | 49 | 2 | 2 | 67 | 95 | 106 | 146 |
| 14. "Miocene," Colombia | 19 | 29 | 1 | 1 | 25 | 44 | 45 | 74 |
| 15. "Miocene," Colombia | 20 | 49 | | | 24 | 43 | 44 | 92 |
| 16. Lower Gatun, Panama | 66 | 73 | 4 | 4 | 119 | 170 | 189 | 247 |
| 17. Middle Gatun, Panama | 107 | 134 | 7 | 8 | 145 | 217 | 259 | 359 |
| 18. Upper Gatun, Panama | 53 | 64 | 6 | 8 | 92 | 98 | 151 | 170 |
| 19. Limon Basin, Costa Rica | 79 | 120 | | | 65 | 147 | 144 | 267 |
| 20. Armuelles, Panama and Costa Rica | 42 | 51 | 1 | 1 | 49 | 62 | 92 | 114 |
| 21. Charco Azul, Panama and Costa Rica | 36 | 50 | 1 | 1 | 55 | 79 | 92 | 130 |
| 22. Angostura, Ecuador | 29 | 32 | | | 48 | 66 | 77 | 98 |
| 23. "Esmeraldas," Ecuador | 33 | 35 | 2 | 3 | 84 | 120 | 119 | 158 |

References: 1, Woodring (1925, 1928); 2–3, Jung (1971); 4–6, Maury (1925); 7, Rutsch (1942); 8–10, Jung (1969); 11–12, Weisbord (1962, 1964); 13, Jung (1965); 14, Weisbord (1929); 15, Barrios (1960); 16–18, Woodring (1957–1982); 19, Olsson (1922); 20–21, Olsson (1942); 22–23, Olsson (1964).

stratigraphic and facies reconnaissance based on common taxa. Due to this more limited sampling, the median numbers of taxa for the 23 studies listed in Table 1 are only 107 subgenera and 135 species.

Failure to consider the limited and inconsistent sampling among these studies, coupled with imprecise and sometimes faulty stratigraphy, has led to highly erroneous interpretations of patterns and trends of molluscan diversity in space and time throughout the region. Numerous authors concluded, for example, that numbers of molluscan taxa declined dramatically in the tropical western Atlantic during the Pliocene (Woodring, 1966; Vermeij, 1978; Stanley and Campbell, 1981; Jones and Hasson, 1985; Stanley, 1986; Vermeij and Petuch 1986). Furthermore, they attributed these supposed changes to oceanographic consequences of the rise of the Isthmus of Panama or intensification of glaciation in the Northern Hemisphere. However, their data were strongly biased by much greater sampling of Miocene and Early Pliocene compared with Late Pleistocene to recent faunas. More recent and extensive sampling of younger faunas demonstrates that diversity did not decrease (Allmon *et al.*, 1993, 1996; Roy *et al.*, 1995, 1998) and may have increased (Jackson *et al.*, 1993). Rates of extinction and origination intensified greatly towards the end of the Pliocene, but these processes were roughly balanced so that total numbers of taxa effectively stayed the same.

This paper describes the analysis of 245 collections of fossil mollusks from the Limon Basin of Costa Rica and the Bocas del Toro and Panama Canal basins of Panama that range in age from approximately 11.6 to 1.4 million years. The PPP occurrence data are available at the internet site http://www.fiu.edu/˜collinsl/. Our goals are to:

1. describe in detail how the collections were made and assess possible biases in sampling, processing, identification and analysis;
2. compare collections broken down by basins of deposition, age, and environment to determine how well we sampled the total diversity at any age, place or water depth, and the adequacy of these data to assess trends in diversity over time;
3. identify common taxa in the collections and their patterns of association in space and time based on ordination analyses; and
4. use correlations of ordination scores with age and water depth to estimate the relative importance of age and environment to variations in faunal composition over 10 million years.

Throughout the paper, we emphasize problems of sampling and taxonomy to demonstrate what we believe is required to rigorously establish faunal patterns and trends. The amount of work required is enormous and much still remains to be done. Nevertheless, it is already possible to recognize consistently common taxa and draw conclusions about the stability of diversity over time. Future papers will build on these results to examine changes in rates and selectivity of extinction and origination, taxonomic composition, body size, shell thickness and ornamentation, incidence of predation, and the proportions of different functional groups defined on the basis of life habits and diet.

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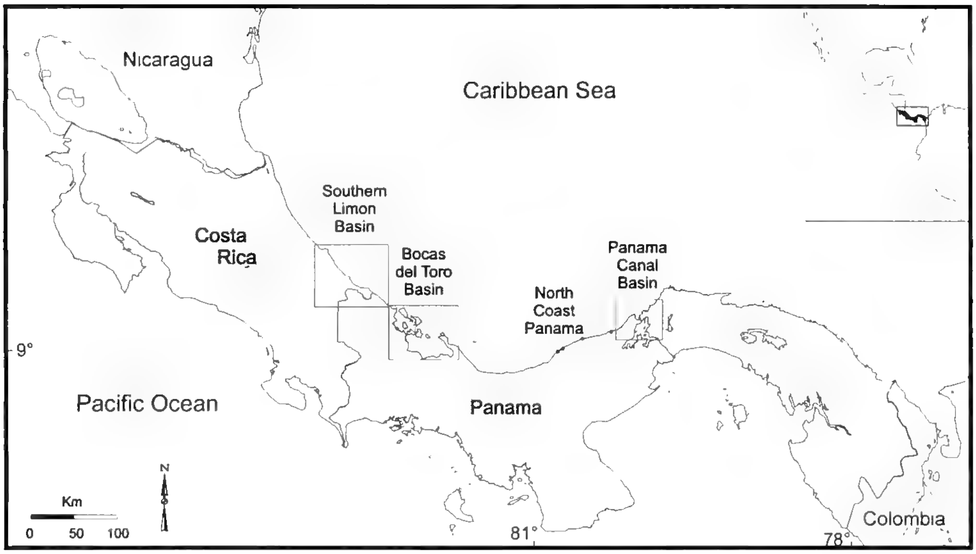
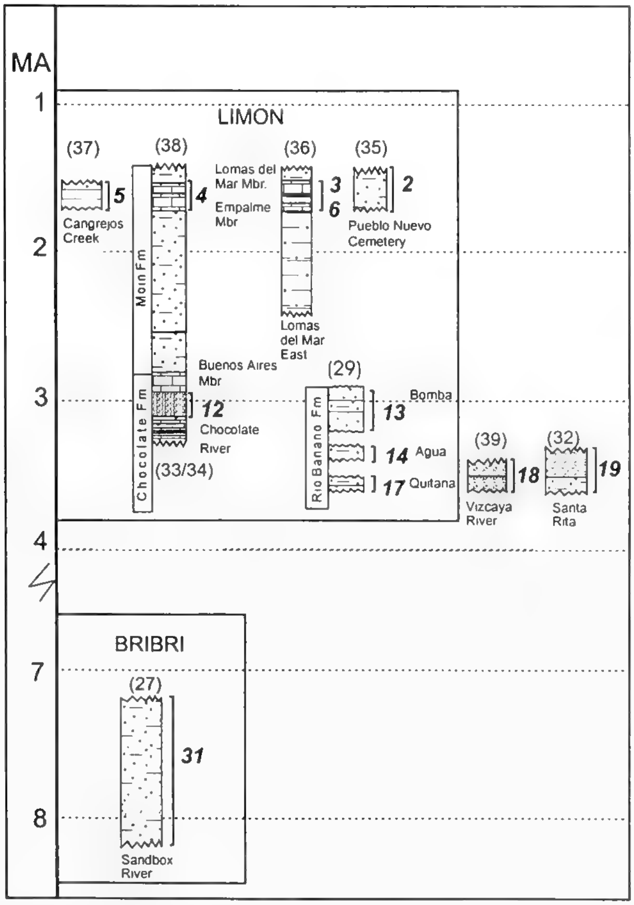
Tony Coates measured the sections and developed the entire stratigraphic framework for the PPP upon which this study is based. Age determinations were provided by Marie-Pierre Aubry, Bill Berggren, Laurel Bybell, Harry Dowsett and Don McNeill, and coordinated by Laurie Collins, who also provided the paleodepth information. Tony Coates, Laurie Collins, Tim Collins, Antoine Heitz, René Panchaud, Jorge Obando, David West, Yira Ventocilla and a great many others helped with the fieldwork. Magnolia Calderón, Antoine Heitz, Karl Müller, and Yira Ventocilla processed the samples. René Panchaud and Antoine Heitz curated and managed the collections at the Naturhistorisches Museum (NMB) in Basel, Switzerland. Felix Wiedenmayer created the database for all of the NMB Venezuelan and Trinidadian collections. Winifred and Jack Gibson-Smith assisted greatly in the original identifications. Xenia Guerra prepared figures 1–5. Discussions with Ann Budd and Alan Cheetham helped to organize our thoughts about so many taxa, and reviews by Lee-Ann Hayek, Carl Koch and Geerat Vermeij greatly improved the manuscript. This work was supported by grants from the Kuglerfonds of the NMB, National Geographic Society, Scholarly Studies and Walcott Funds of the Smithsonian Institution, Schweizerischer Nationalfonds Forschung (Grant Numbers 21-36589.92 and 20-43229.95), U. S. National Science Foundation (Grant Numbers BSR90-06523, DEB-9300905, DEB-9696123, and DEB-9705289), the NMB, and the Smithsonian Tropical Research Institute.

## STRATIGRAPHY, COLLECTIONS AND TAXONOMY

Any study of the distribution and abundance of fossil taxa depends upon the quality and consistency of four basic factors: (1) stratigraphic control in space and time, (2) independent paleoenvironmental analysis, (3) methods of collection and processing of samples, and (4) identification of taxa.



Text-figure 2.—Map of Panama and Costa Rica showing the locations of the four areas sampled for this paper.

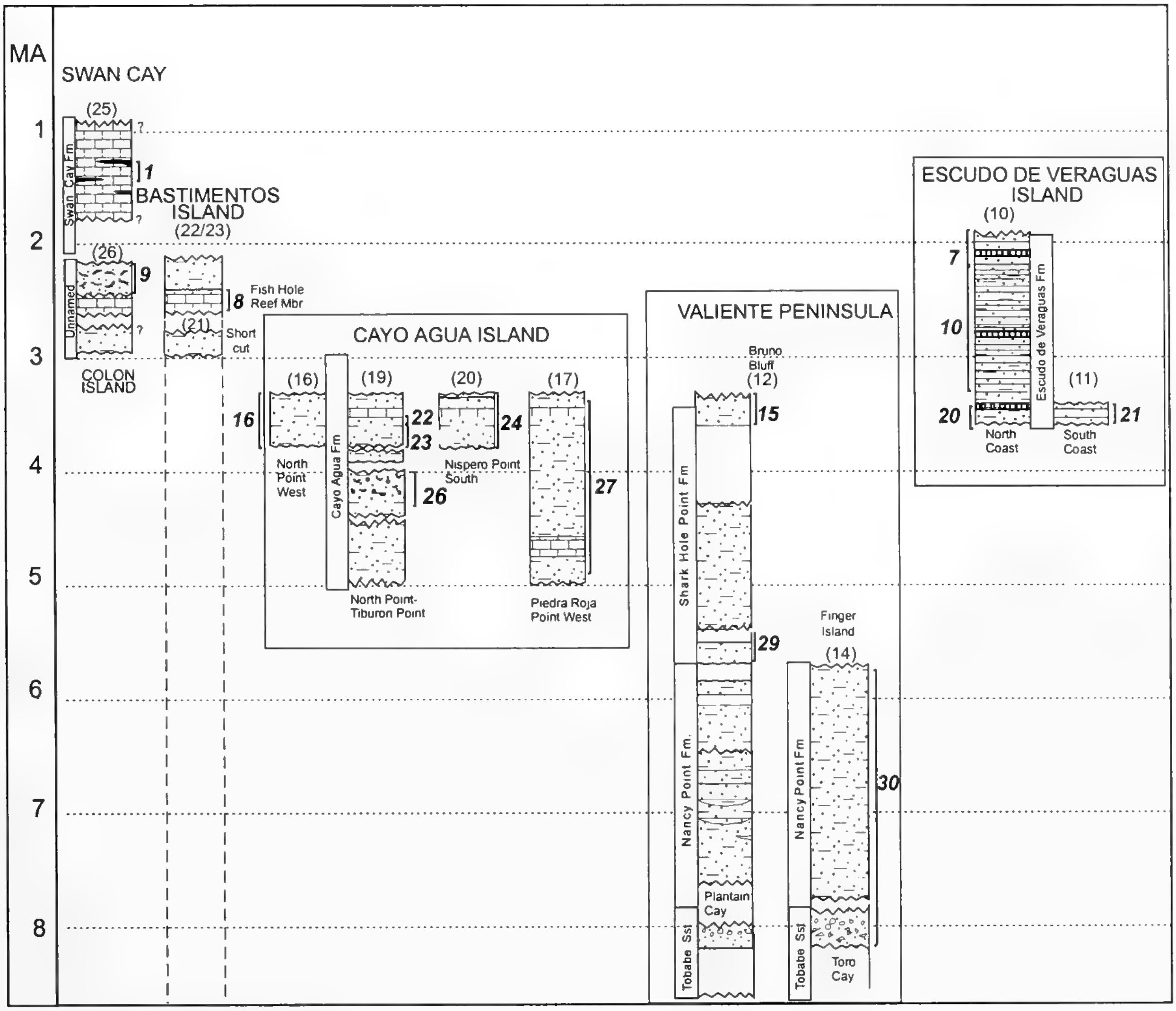


Text-figure 3.—Summary of the stratigraphy of the Limon Basin for all sections sampled for this paper. Numbers in parentheses above stratigraphic columns are section numbers (Coates, this volume, Chapter 1). The stratigraphic position of each molluscan faunule is shown by numbers in boldfaced italics.

## STRATIGRAPHY

The 245 collections analyzed in this paper come from three small, adjacent basins along the Caribbean coast of southeastern Costa Rica to central Panama (Text-fig. 2; Coates *et al.,* 1992; Coates and Obando, 1996; Coates, Chapter 1, Appendix A, this volume). Most ages used for this paper are medians of age ranges that were defined using planktic foraminifera, calcareous nannofossils and (for the Limon Basin only) paleomagnetics (App. 1; Bybell, Chapter 2, this volume; Cotton, Chapter 3, this volume; Aubry and Berggren, Appendix 1 in Chapter 1, this volume; McNeill *et al.,* in press). Ages of two sets of undated collections from Isla Popa and Rio Tuba were assumed to be equivalent to nearby dated horizons at Cayo Agua and Rio Sand Box respectively based on stratigraphic position. In addition, very approximate ages ("Late Pliocene" and "Late Miocene") were arbitrarily assigned to three sets of undated collections from Ground Creek, Rio Calzones and Miguel de la Borda based on inferred field relationships. Medians of all these inferred ages are given in brackets to emphasize their uncertainty.

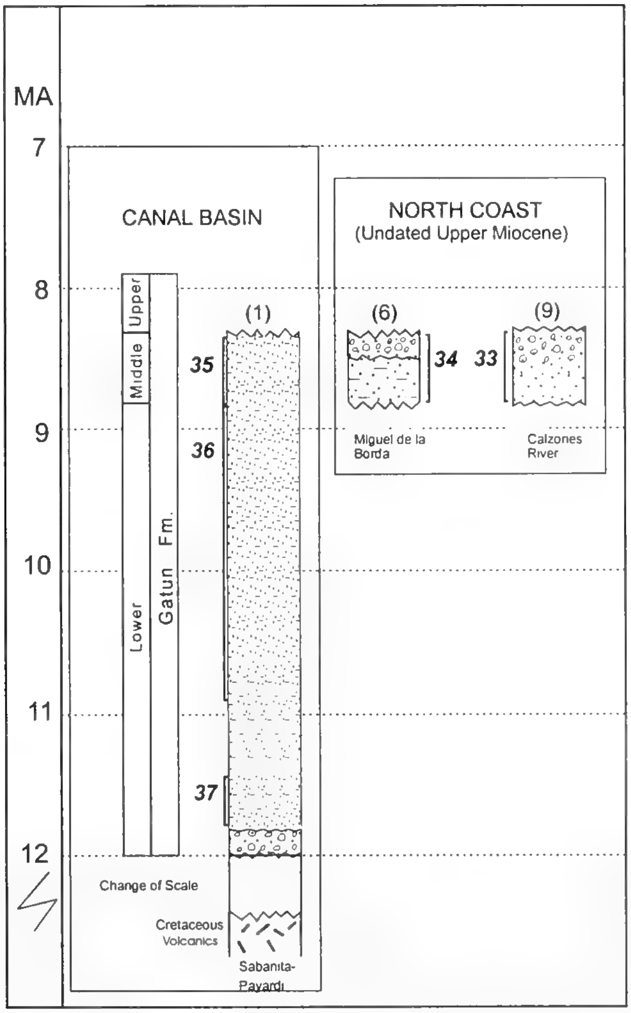
The 103 collections from the Limon Basin range in age from late Late Miocene (7.7 Ma) at Rio Sand Box to near the Plio–Pleistocene boundary (1.6 Ma) at Lomas del Mar (Text-fig. 3; Appendix B, this volume). However, the great majority of the collections come from the late Early to early Late Pliocene Rio Banano Formation, the earliest Late Pliocene Quebrada Chocolate Formation and the basal Pleistocene Moin Formation. The 96 collections from the Bocas del Toro Basin also range from late Late Miocene (6.9 Ma) at



Text-figure 4.—Summary of the stratigraphy of the Bocas del Toro Basin for all sections sampled for this paper. Section numbers and faunule numbers shown as in Text-figure 3.

Finger Island on the Valiente Peninsula to Early Pleistocene (1.4 Ma) at Swan Cay; but the collections are more evenly distributed in age than in the Limon Basin (Text-fig. 4; Appendix B, this volume). The 46 collections from the Canal Basin are all Late Miocene (Text-fig. 5), ranging from the lower Gatun Formation at the Martin Luther King housing development (11.6 Ma) to the middle Gatun Formation at Isla Payardi (9.0 Ma). There are no collections so far from the mollusk-rich Rio Indio facies (*sensu* Collins *et al.*, 1996) of the Late Miocene (mostly 6.4–5.8 Ma) Chagres Formation. Finally, the three collections from the north-central coast of Panama are as yet undated but are very probably Late Miocene.

The stratigraphy of all three basins and the strengths and weaknesses of the age dating are discussed in detail elsewhere in this volume. Here we only consider possible problems of particular relevance to the mollusks. In the Limon Basin, the entire Rio Banano Formation, including the section from Quitaria through La Bomba, is now considered to be 3.6–2.9 Ma (McNeill *et al.*, in press). Previously, La Bomba had been dated at 2.4–2.5 Ma (Coates *et al.*, 1992), but it is now considered to be 3.1 Ma. In addition, the sequence of coral reef tracts, flank deposits and inter-reef basins extending westward from Limon is now known to range from 1.7–1.5 Ma at Lomas del Mar to 3.6–3.3 Ma at Quebrada Chocolate, and there is also a patch reef within the Rio Banano sequence at Brazo Seco tentatively dated at 5.2–4.3 Ma (Budd *et al.*, 1996, this volume; Budd and Johnson, 1997; McNeill *et al.*, in press. Immediately west of Limon, the new Quebrada Chocolate Formation replaces the uppermost part of the Rio Banano Formation *sensu* Coates *et al.* (1992). The Que-



Text-figure 5.—Summary of the stratigraphy of the Canal Basin and central north coast of Panama for all sections sampled for this paper. Section and faunules numbers shown as in Text-figure 3.

brada Chocolate Formation overlaps in age with the Rio Banano Formation at the latter's type locality at Bomba. Finally, the age and stratigraphic position are still uncertain for the mollusk-rich deposits at Pueblo Nuevo, the Cementerio General and the Progressive Baptist Church, although they are probably the same age as Lomas del Mar.

Ages of formations in the Bocas del Toro Basin have remained more stable, and the principal developments are the inclusion of numerous new, mollusk-rich horizons that fill important gaps in the sequence. The most important included here are the Late Pliocene to Early Pleistocene horizons at Fish Hole, Ground Creek and Swan Cay in the northwest and Late Miocene Finger Island in the southeast. Finally, the age of the important Gatun Formation in the Panama Canal Basin now extends back to the uppermost Middle Miocene (11.8–11.4 Ma) (Collins *et al.*, 1996) instead of 8.2 Ma (Coates *et al.*, 1992).

## PALEOENVIRONMENTAL ANALYSIS

It is essential to identify environments independently of the mollusks to avoid circular reasoning. The most complete paleoenvironmental data available so far are for water depth, based primarily on benthic foraminifera, but also ostracodes, otoliths and ahermatypic corals (Appendix 1; Collins *et al.*, Chapter 4). These data are available for 29 of the 37 depths used herein. The remainder were assigned conservatively based on regional stratigraphic and facies relationships pending analysis of benthic foraminifera. Detailed sedimentary facies analyses have not yet been attempted.

## COLLECTIONS

Our basic sampling unit is a collection, which we define as the sum total of all the samples of fossils collected at one time from some stratigraphically well defined horizon at a single location. Subsequent collections from exactly the same site are given a new collection number. Most of our collections from the Limon Basin come from river banks and new construction sites; from the Bocas del Toro Basin they are primarily from sea cliffs; and from the Panama Canal Basin they are from new construction sites. In the latter case, the great majority of Woodring's (1957–1982) original localities are gone.

The process of assembling a collection is a long and commonly iterative process. The problem is that no one method is suitable for collecting all the mollusks at a site, primarily because of differences in size and preservation. We therefore collect two kinds of samples, which we call "specimen" and "bulk." Specimen samples comprise all of the visible shells at the outcrop that can be collected individually in place from the outcrop or as float at the immediate base of the outcrop. Bulk samples are typically 10-kg sacks of sediment that are excavated for future processing at the laboratory. Specimen and bulk samples are given numbers in the field according to the individual investigator's system, but these subsequently are assigned PPP numbers, which are used hereout for convenience and accuracy of comparison.

Specimen and bulk samples are subject to numerous sources of bias, which we try to avoid through use of standard methods. Factors, which affect both types of sample, are the condition of the material and the amount of time and number of collectors available. For example, to make one collection at a single small, but rich, site may require four experienced collectors an entire afternoon. Moreover, as we shall see, no single collection contains more than an indeterminate small fraction of the total fauna at a site as can be observed after repeated collecting.

Two additional factors that affect the usefulness of the specimen collections are care in individually wrapping and packing the specimens at the outcrop or in camp and investigator bias. Specimens are wrapped in tissue, packed, sealed in cans or other rigid containers, and then repacked for eventual shipment to Basel. In addition, comparison of our own and earlier collections from the same sites repeatedly demonstrates that many earlier collections were biased in favor of large, pretty snails at the expense of bivalves, smaller snails and unattractive or fragile fossils in general.

The most important additional factor affecting the quality of the bulk samples is the depth of excavation before taking a sample. Most of our collections come from volcaniclastic silty sands to sandy silts that are gray to dark brown at the weathered, outcrop surface but a highly distinctive slate blue-gray when fresh. It is commonly necessary to excavate at least 0.5 m beneath the outcrop surface to encounter fresh material, except after fortuitous floods or storms excavate riverbanks and coastal cliffs en masse. Digging "to the blue" may require an hour or more per sample, but the resulting numbers of taxa collected in a single bulk sample may increase more than two-fold, accordingly. Finally, the number of bulk samples made at any site depends on available time and energy as well as the apparent richness of the material. One bag of bulk sediment is routinely collected at most sites, but 3 to 10 bags are collected where the material is rich in fossils.

Processing of specimen samples is mostly a matter of routine museum curation. All collections are assigned a Naturhistorisches Museum of Basel (NMB) number but are stored separately in cabinets arranged by sedimentary basin and PPP number. In contrast, processing of bulk samples is more complex and time consuming. The same bulk samples are processed for corals, bryozoans, otoliths, fish and shark teeth, echinoderms and brachiopods, as well as for mollusks. Therefore, three sizes of sieve openings are used: 2000, 500 and 125 μm. Our goal is to process and pick mollusks from the 2000-μm (2-mm) fraction from at least one bulk sample from every collection. However, this task was not completed for two thirds of the collections for inclusion in this paper. The 500-μm fraction contains many micromollusks and the larval shells of larger species. These micromollusks are commonly extremely abundant and diverse, but thousands of additional hours would be required just to pick them, and they are a separate study in themselves.

Washing and diasaggregation (processing) of the bulk samples is done as gently as possible. Sometimes it is unnecessary to do more than soak the sample in water before sieving, but other times it is necessary to use detergent, hydrogen peroxide or to heat and freeze the sample. The latter treatments inevitably damage some specimens, but the condition and diversity of the material so far obtained suggests little more damage occurs than is sustained through wet sieving. All picking is done at 10× magnification using a Wild M-5 stereomicroscope. Fossils from the bulk samples are curated and stored in the same drawers as the corresponding specimen samples.

## TAXONOMY

It cannot be overemphasized that the superspecific taxonomy and systematics are poorly resolved for the majority of Neogene and Quaternary mollusks of tropical America. Diagnostic characters of many of the commonest genera or subgenera are not consistently stated or applied, and only a handful of taxa have been analyzed cladistically to help clarify relationships. Similar problems apply to species, which are commonly assigned names uncritically based on comparison with monographs of other faunas, without examining the types, a practice that produces misinformation rather than precision (Robinson, 1993; Waller, 1993).

We conservatively estimate that more than half of the species in our collections are undescribed, and that it would require a decade or more to describe them properly group by group. We base this estimate on results of recent and ongoing studies of the few common groups so far examined in detail throughout the region. These include the *Strombina* Group (Jung, 1989; Jackson *et al.*, 1996; Fortunato and Jackson, unpublished data); Muricidae (Vokes, 1989; D. Miller, unpublished data), Turridae (J. Todd, unpublished data), and *Tucetona* (P. Tschudin, unpublished data). We therefore adopted the following pragmatic policy for the preliminary identification of taxa for faunal lists:

1. All identifications are at the generic or subgeneric level.
2. Great effort is devoted to establishing lists of characters for the consistent recognition of genera and subgenera, with the greatest emphasis paid to the roughly 200 genera or subgenera that make up more than 90% of the specimens (Appendix 2). Many of these taxa may prove to be polyphyletic in subsequent systematic study, but they will have been identified consistently so that the data will be useable should future study of strict monophyla be desirable.
3. A reference collection is being established for common taxa that includes diagnostic characters and specimens from each of the sedimentary basins and ages where the genus or subgenus occurs (broken

down as Late Miocene, Pliocene, and Pleistocene from each of the three basins). Digital images and diagnostic characters of the common taxa are being placed on the World Wide Web site of the Neogene Marine Biota of Tropical America (NMITA) taxonomic database system (http://nmita.geology.uiowa.edu).

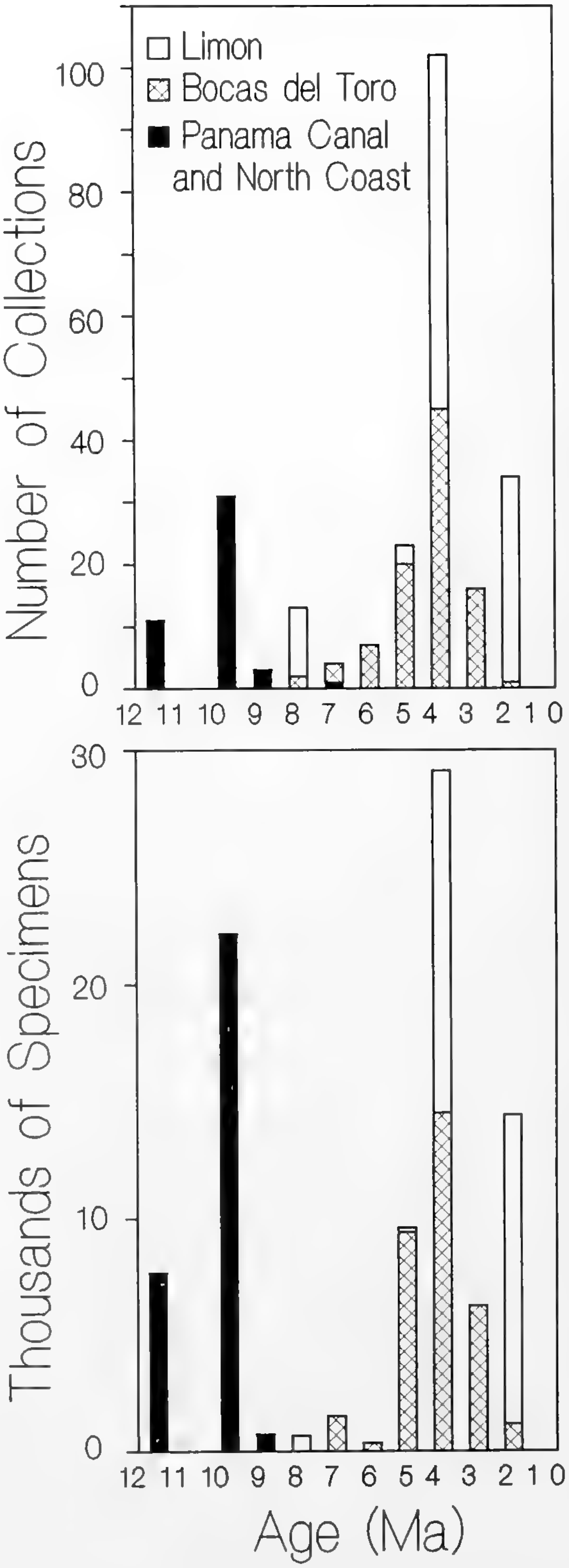
4. No attempt was made to revise (even informally) numerically important problematic taxa such as *Turritella, Anadara* (*Rasia*), and most of the turrids due to lack of time, even though they almost certainly include numerous, unrecognized subgenera or even genera. This lack of resolution inevitably reduces our initial estimates of diversity. On the other hand, about one third of the taxa (almost all of them rare) are questionably identified due to problems of preservation or inadequate published descriptions, which inflates our estimates because questionable identifications are listed separately in the database.

Following these guidelines, specimens in each collection were identified to genus or subgenus and counted. Because of the difference in effort and time involved, identifications and tabulations of taxa were usually completed for the specimen samples from a given locality long before the bulk samples were processed from the same locality. Mollusks from the bulk samples of only one third of the 245 collections have been included with material from the specimen samples in the following analyses.

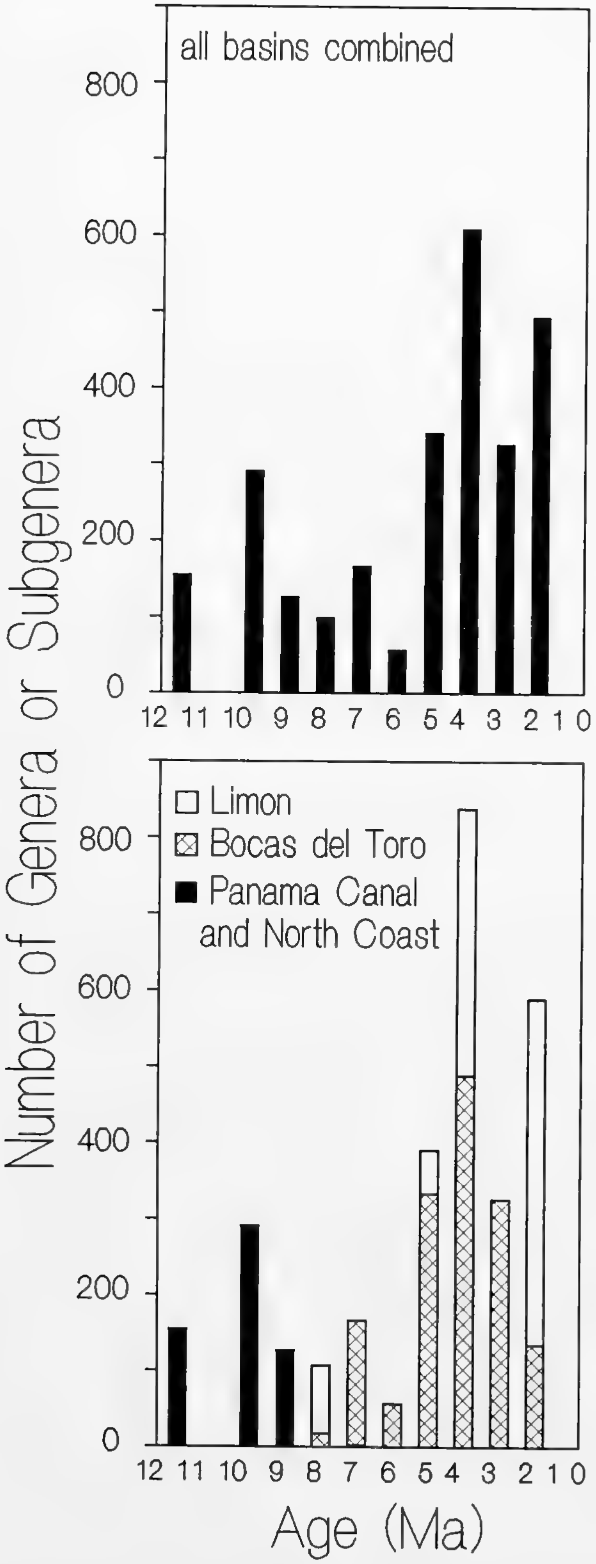
## DISTRIBUTION, AGE, AND ADEQUACY OF COLLECTIONS

The numbers of collections and specimens upon which this paper is based are broken down by sedimentary basins and age in Text-figure 6. There are two clear biases in these data. First, the sampling effort is unevenly distributed through time because most of the collections were made in the early stages of the PPP before we were confident of the stratigraphy, and because some ages are better represented than others in the areas studied. Second, space and time are confounded because all the collections younger than 6 Ma come from the two western basins whereas all those older than 8 Ma come from the Canal Basin.

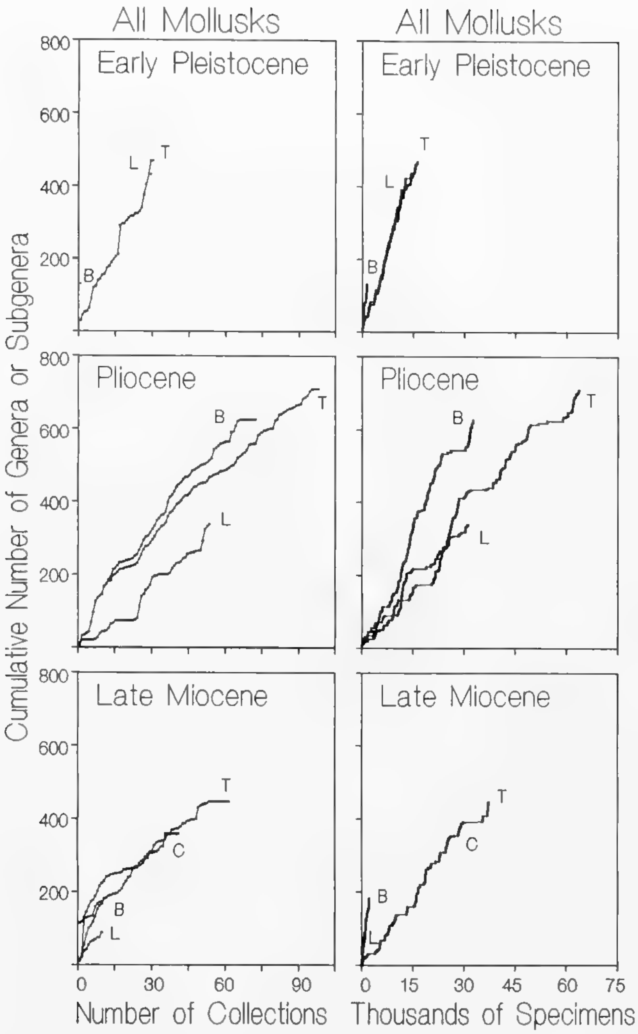
There are similar sampling problems with depths and environments of deposition determined using benthic foraminifera (Appendix 1). Late Miocene mollusks sampled so far from the Canal Basin (11.6–8.6 Ma) were all deposited in only 15–40 m water depth, whereas those from the western basins (7.7–5.7 Ma) range from 60–200 m. Pliocene and Pleistocene de-



Text-figure 6.—Numbers of collections and thousands of specimens per million years for each sedimentary basin. Each collection was assigned to one age interval using the median of the estimate of the age.



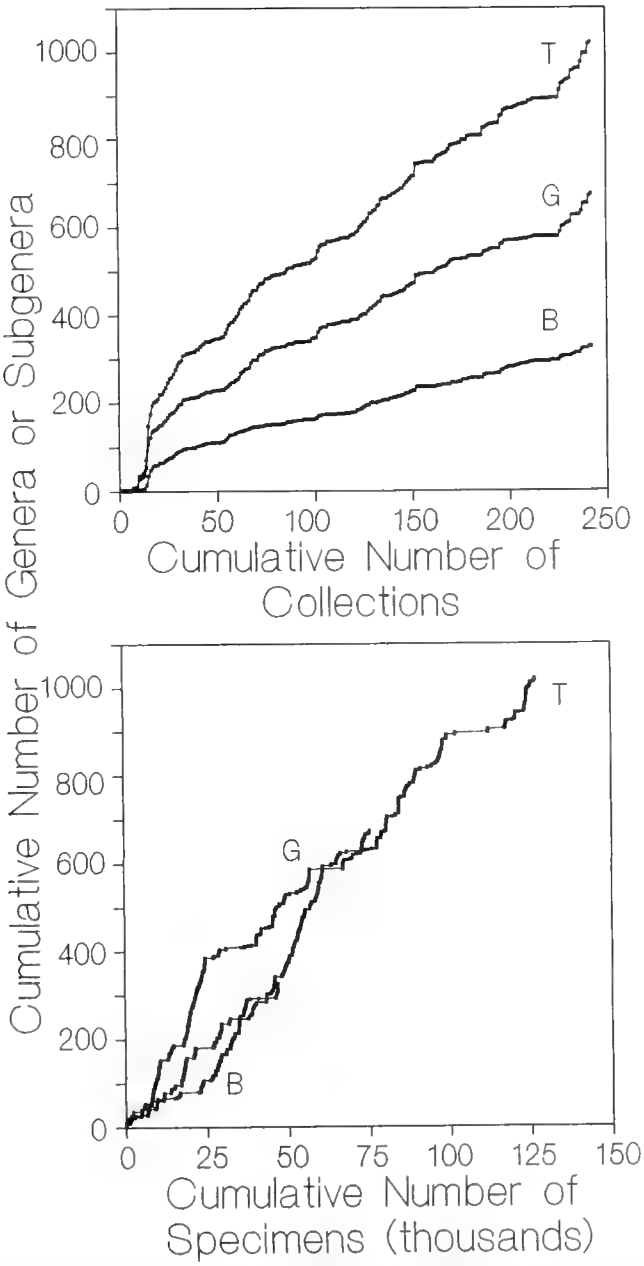
Text-figure 7.—Numbers of genera or subgenera per million years for all sedimentary basins combined and for each separate basin. The totals are larger for the separate basins because many taxa occur in more than one basin.



Text-figure 8.—Cumulative numbers of genera and subgenera collected as a function of both the numbers of collections made and numbers of specimens accumulated for three time intervals (Late Miocene, Pliocene, and Early Pleistocene). L = Limon basin, B = Bocas del Toro Basin, C = Canal Basin and Panama north coast, T = total for all basins combined.

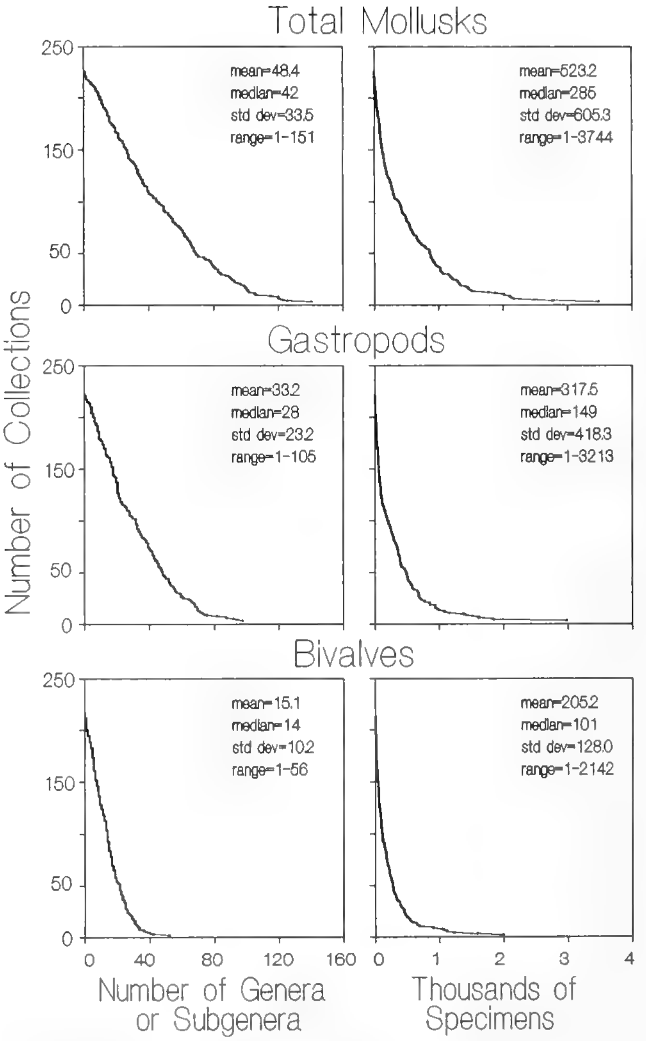
posits from both of the western basins include a better mix of environments ranging from about 10–200 m.

Numbers of genera and subgenera collected closely parallel the sampling effort (Text-fig. 7), which strongly suggests that a large fraction of taxa from each age interval is uncollected (Koch, 1987). This is confirmed by the steep increase in cumulative numbers of taxa as a function of the numbers of collections or specimens, whether broken down by age and basin (Text-fig. 8), or for all 245 collections combined (Text-fig. 9). The reasons for these daunting results are that most collections contain comparatively few specimens or taxa (Text-fig. 10) and, as expected in the tropics (Sanders, 1969), most taxa are extremely rare (Text-fig. 11). Half of the 1021 genera or subgenera are rep-



Text-figure 9.—Cumulative numbers of genera or subgenera collected as a function of both the numbers of collections made and numbers of specimens accumulated for all 245 collections combined. B = bivalves, G = gastropods, T = total mollusks (includes bivalves, gastropods and scaphopods).

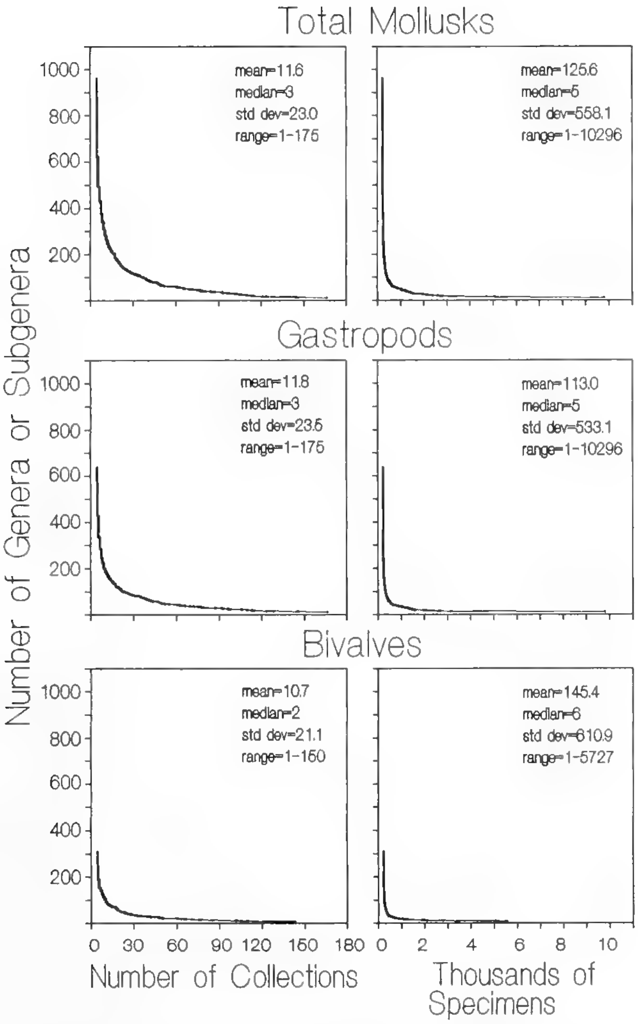
resented by fewer than five specimens from fewer than three collections. Nevertheless, subgeneric to generic diversity per basin per million years in our PPP collections (Text-fig. 7) generally exceeds that obtained in most of the studies listed in Table 1.



Text-figure 10.—Frequency distributions of numbers of taxa and specimens per collection for total mollusks (including scaphopods), and for gastropods and bivalves each taken alone.

## COMPOSITION OF THE FAUNA

There are a total of 149 families and 1021 genera or subgenera of mollusks in the 245 collections that break down as summarized in Table 2. The proportions of genera or subgenera for gastropods, bivalves and scaphopods (0.66:0.32:0.02) are broadly similar to those reported in the faunas listed in Table 1. This suggests that the PPP collections are not biased somehow in the representation of these three major taxa. Only 156 out of the total 1021 genera and subgenera are represented by 100 or more specimens in the 245 collections (listed in descending order in Appendix 2). These include 96 gastropods, 52 bivalves and 8 scaphopods. The abundance of some of these, such as *Turritella* and *Anadara* (*Rasia*), is clearly artificially high due to taxonomic lumping. In contrast, abundances of most of the smaller taxa (including the top three bivalves *Crassinella, Caryocorbula* and *Varicorbula*) are too low because specimens from bulk sam-



Text-figure 11.—Frequency distributions of numbers of collections and numbers of specimens per genus or subgenus for total mollusks, gastropods and bivalves.

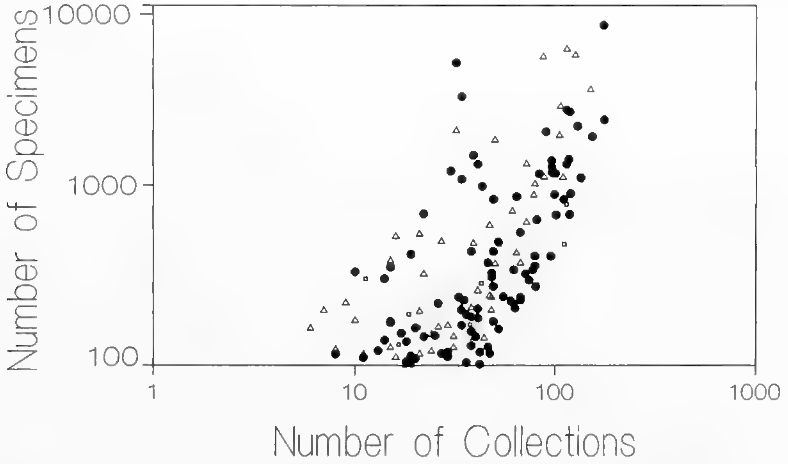
Table 2.—Composition of the molluscan fauna from 245 collections of fossils.

| Taxa | Numbers of families | Numbers of genera and subgenera |
|---|---|---|
| Gastropoda | 89 | 675 |
| Bivalvia | 54 | 326 |
| Scaphopoda | 7 | 19 |
| Cephalopoda | 1 | 1 |
| Totals | 149 | 1021 |

ples have not been processed for two thirds of the collections.

As expected for such data (Williams, 1964; Hanski *et al.*, 1993; Hayek and Buzas, 1997), there is a strong positive correlation between the abundance of these 156 commonest taxa, as measured by numbers of specimens (range 100 to 10,296), and their frequency of occurrence in the different collections (range 3 to 175) (Spearman rank-order correlation, r = +0.669, P < 0.000; Text-fig. 12). Nevertheless, there is considerable variation in frequency. Many taxa of closely similar abundance exhibit a 5- to 10-fold range in the numbers of collections in which they occur. These differences reflect the relative eurytopy or stenotopy of taxa (Jackson, 1974). For example, 407 *Volvulella* (*Volvulella*) occur in 95 collections, whereas the scaphopod *Gadilopsis* occurs as 435 specimens in only 11 collections. Likewise, 1104 *Polystira* are distributed among 134 collections, whereas the next most abundant taxon *Sincola* (*Sincola*) is represented by 1085 specimens from only 34 collections. In both cases, the more narrowly distributed taxa are limited to shelf envionments whereas more widespread taxa occur in a greater diversity of environments.

The156 most common gastropods, bivalves and sca-



Text-figure 12.—Logarithmic plot of numbers of specimens versus numbers of collections for all genera or subgenera represented by 100 or more specimens in all collections combined as listed in Appendix 2. Filled circles = gastropods, triangles = bivalves, and squares = scaphopods.

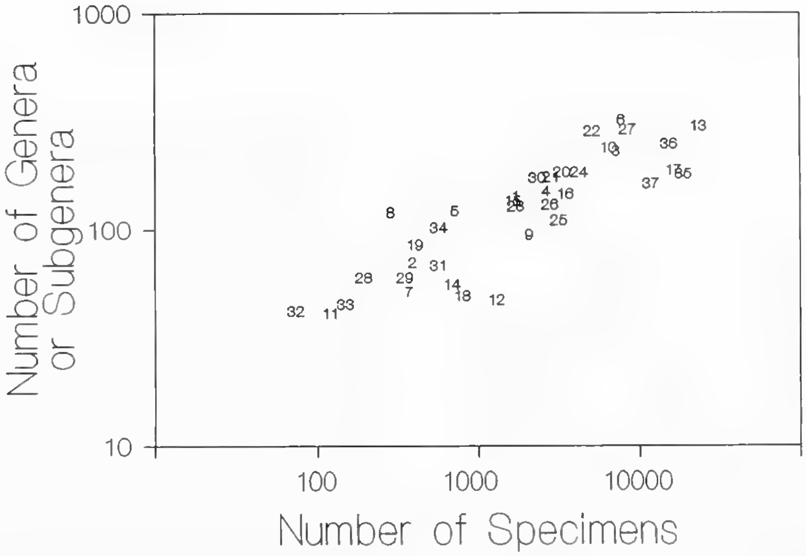
Table 3.—List of 37 faunules (molluscan taxa from a single horizon at a single outcrop or closely grouped outcrops) and descriptive statistics used for the ordination analyses. Taxa are genera or subgenera. Lists of PPP numbers for each faunule are given in Appendix 3. Documentation for ages and depths are given in Appendix 1. Estimated ages and depths placed in brackets. L = Limon Basin, B = Bocas del Toro Basin, NC = North Coast of Panama, C = Panama Canal Basin.

| Faunule number | Faunule name | Basin | Section number | Median age | Median depth | Number of collections | Number of specimens | Number of taxa | Fisher's alpha |
|---|---|---|---|---|---|---|---|---|---|
| 1 | Swan Cay | B | 25 | 1.4 | 100 | 1 | 1,418 | 135 | 36.691 |
| 2 | Cemetery Pueblo Nuevo | L | 35 | 1.6 | 75 | 1 | 452 | 67 | 21.744 |
| 3 | Upper Lomas del Mar east (reef) | L | 36 | 1.6 | 75 | 12 | 5,986 | 219 | 44.637 |
| 4 | Empalme | L | 34 | 1.6 | 20 | 5 | 2,188 | 143 | 34.508 |
| 5 | Cangrejos Creek | L | 37 | 1.6 | 200 | 5 | 828 | 116 | 36.734 |
| 6 | Lower Lomas del Mar east (non-reef) | L | 36 | 1.7 | 75 | 10 | 6,458 | 304 | 66.229 |
| 7 | Northwest Escudo de Veraguas | B | 10 | 2.0 | 125 | 4 | 433 | 49 | 14.206 |
| 8 | Fish Hole | B | 22/23 | 2.6 | 70 | 3 | 331 | 114 | 61.516 |
| 9 | Ground Creek | B |  | [2.6] | [50] | 2 | 1,723 | 90 | 20.283 |
| 10 | North central Escudo de Veraguas | B | 10 | 2.8 | 125 | 8 | 5,019 | 227 | 48.916 |
| 11 | Rio Limoncito | L |  | 3.0 | [30] | 1 | 148 | 39 | 17.269 |
| 12 | Chocolate Buenos Aires | L | 33 | 3.1 | [50] | 3 | 1,011 | 45 | 9.657 |
| 13 | Bomba | L | 29 | 3.1 | 30 | 34 | 18,181 | 285 | 47.980 |
| 14 | Agua | L | 29 | 3.3 | 30 | 2 | 841 | 53 | 12.565 |
| 15 | Bruno Bluff | B | 12 | 3.5 | 175 | 4 | 1,310 | 133 | 35.822 |
| 16 | Cayo Agua: west side Punta Norte | B | 16 | 3.5 | 30 | 8 | 2,715 | 139 | 31.238 |
| 17 | Quitaria | L | 29 | 3.5 | 30 | 7 | 12,690 | 179 | 29.508 |
| 18 | Rio Vizcaya | L | 39 | 3.5 | 25 | 7 | 979 | 47 | 10.296 |
| 19 | Santa Rita | L | 32 | 3.5 | 30 | 2 | 497 | 81 | 27.462 |
| 20 | Northeast Escudo de Veraguas | B | 10 | 3.6 | 125 | 4 | 2,588 | 175 | 42.847 |
| 21 | Southeast Escudo de Veraguas | B | 11 | 3.6 | 125 | 9 | 2,215 | 166 | 41.888 |
| 22 | Cayo Agua: Punta Tiberon | B | 19 | 3.6 | 60 | 9 | 4,001 | 270 | 65.368 |
| 23 | Cayo Agua: Punta Nispero west | B | 19 | 3.6 | 60 | 6 | 1,339 | 122 | 32.648 |
| 24 | Cayo Agua: southeast Punta Nispero | B | 20 | 3.6 | 60 | 7 | 3,307 | 175 | 39.562 |
| 25 | Isla Popa | B |  | [4.3] | [60] | 7 | 2,445 | 101 | 22.431 |
| 26 | Cayo Agua: Punta Norte east | B | 19 | 4.3 | 60 | 6 | 2,185 | 124 | 28.663 |
| 27 | Cayo Agua: Punta Piedra Roja west | B | 17 | 4.3 | 43 | 6 | 6,640 | 275 | 57.881 |
| 28 | Quebrada Brazo Seco | L |  | 4.8 | [50] | 3 | 240 | 57 | 23.632 |
| 29 | Shark Hole Point | B | 12 | 5.7 | 150 | 7 | 432 | 57 | 17.586 |
| 30 | Finger Island | B | 14 | 6.9 | 80 | 3 | 1,817 | 165 | 44.354 |
| 31 | Rio Sand Box and Hone Creek | L | 27 | 7.7 | 175 | 6 | 697 | 65 | 17.534 |
| 32 | Rio Tuba | L |  | [7.7] | [175] | 5 | 91 | 40 | 27.279 |
| 33 | Rio Calzones | NC | 9 | [8.3] | [25] | 2 | 185 | 43 | 18.598 |
| 34 | Miguel de la Borda | NC | 6 | [8.3] | 25 | 1 | 699 | 97 | 30.580 |
| 35 | Isla Payardi | C | 1 | 9.0 | 28 | 14 | 14,627 | 172 | 27.376 |
| 36 | Mattress Factory | C | 1 | 9.0 | 28 | 16 | 11,957 | 236 | 41.677 |
| 37 | Martin Luther King Jr. | C | 1 | 11.6 | 28 | 11 | 9,242 | 155 | 26.455 |

phopods also differ in the median numbers of collections in which they occur. The median for the 96 gastropod taxa is 46.5 collections, the median for the 52 bivalve taxa is 36 collections, and the median for the eight scaphopod taxa is 28 collections (Kruskal-Wallis test, chi-square = 4.89, d.f. = 2, P = 0.087). These marginally significant results suggest that common gastropods were more eurytopic than bivalves, which were, in turn, more eurytopic than scaphopods.

## FAUNAL ASSEMBLAGES

The median numbers of specimens and taxa per collection are small (285 and 42, respectively), and there is enormous variation in the richness of individual collections (Text-fig. 10). We therefore assembled the 245 collections into 37 groups called "faunules" to try to decrease the effects of sample size for the analysis of patterns and trends in diversity and composition of faunal assemblages (Table 3; Text-figs. 3–5). The groupings were made based on age and location. Faunules correspond to a single fossiliferous stratigraphic horizon at a single outcrop (*e.g.*, Swan Cay or Finger Island; Text-fig. 4). Due to pervasive bioturbation at the great majority of sites, bedding could not usually be observed. Therefore, packages of lithologically identical sediment, typically amounting to a few me-



Text-figure 13.—Numbers of genera or subgenera versus numbers of specimens for the 37 faunules listed by the same numbers in Table 3.

ters of section, were treated as a single horizon. Nearby but physically separate outcrops of the same stratigraphic horizon were treated as separate faunules for purposes of replication in the analyses. Examples of replicate faunules include exposures on different headlands of the 3.5–3.6 Ma horizon of the Cayo Agua Formation (Faunules 16, 22, 23 and 24) or the 9.4–8.6 Ma horizon of the Gatun Formation (Faunules 35 and 36) (Text-figs. 4, 5).

The mollusks contained in the 37 faunules range from a minimum of 91 to a maximum of 18,181 specimens, and from 39 to 304 genera or subgenera (medians: 1723 specimens and 124 subgenera per faunule; Table 3). These numbers are large enough to include all of the faunules in analyses of faunal patterns in space and time. Nevertheless, most of this variation in numbers of specimens and taxa is still due to differences in sampling effort, as demonstrated by the highly significant positive correlation between numbers of taxa and specimens among the 37 faunules (Spearman rank order correlation, $r = +0.889$, $P < 0.000$; Text-fig. 13).

## DIVERSITY OF FAUNULES

We used Fisher's alpha as the best single index of diversity because of great differences in sample size among both the faunules (Text-fig. 13) and the one-million-year intervals (Text-figs. 6–7) (Magurran, 1988; Rosenzweig, 1995; Hayek and Buzas, 1997). Use of alpha is based on the assumption that the abundances of species fit a log-series distribution (Fisher *et al.,* 1943), in which case alpha is independent of the number of specimens. Alpha also can be used as a measure of diversity when the log series is not a good statistical fit to the data if the ratio of numbers of specimens to taxa $(N/S) > 1.44$ (Hayek and Buzas, 1997). This was always true for our data. Estimates of alpha for faunules and one-million-year intervals with fewer than 5000 specimens were obtained from Appendix 4 in Hayek and Buzas (1997). Estimates for those with more than 5000 specimens were kindly provided by Lee-Ann Hayek (written commun., 1997, 1998).

Values of alpha for the 37 faunules range more than six-fold, from a low of 9.7 at Chocolate Buenos Aires to a high of 67 at lower Lomas del Mar (median for the 37 faunules = 30.6; Table 3). Alpha is positively correlated with the number of specimens in the faunules (Spearman rank-order correlation, $r = +0.549$, $P = 0.000$), but not so strongly as the number of genera or subgenera with the number of specimens (Text-fig. 13). Alpha also increases nonsignificantly with increasing depth ($r = +0.216$, $P = 0.100$ for 1-tailed test. The 1-tailed test is appropriate because molluscan diversity increases with depth in Recent seas from nearshore to bathyal environments (Rex, 1981).

The faunules are listed in decreasing order of Fisher's alpha in Table 4, along with information gleaned from the stratigraphic sections (Appendix B, this volume) about the presence of corals. Diversity of molluscan faunules from horizons where corals were common is 50% higher than for faunules without corals (median alphas 41.9 versus 27.4, Mann-Whitney Test, $P < 0.01$). The type of coral does not appear to be particularly important, since diversity is high regardless of whether corals are cemented or free-living, solitary or colonial, or with or without symbiotic zooxanthellae. Abundance of free-living, zooxanthellate corals suggests the presence of extensive seagrass beds

Table 4.—Faunules listed in descending order of Fisher's diversity index alpha. Presence of corals as common to abundant based on descriptions of stratigraphic sections in Appendix B (this volume). Asterisk indicates azooxanthellate corals.

| Fisher's Alpha | Faunule number | Occurrence of corals |
|---|---|---|
| 66.2 | 6 | reef-building |
| 65.4 | 22 | free-living |
| 61.5 | 8 | reef-building |
| 57.9 | 27 | free-living |
| 48.9 | 10 | dense thicket* |
| 48.0 | 13 | |
| 44.6 | 3 | reef-building |
| 44.4 | 30 | |
| 42.9 | 20 | horn* |
| 41.9 | 21 | horn* |
| 41.7 | 36 | |
| 39.6 | 24 | free-living |
| 36.7 | 25 | reef-building |
| 36.7 | 5 | |
| 35.8 | 15 | |
| 34.5 | 4 | reef-building |
| 32.7 | 23 | |
| 31.2 | 16 | free-living |
| 30.6 | 34 | |
| 29.3 | 17 | |
| 28.7 | 26 | |
| 27.5 | 19 | |
| 27.4 | 35 | |
| 27.3 | 32 | |
| 26.5 | 37 | |
| 23.6 | 28 | reef-building |
| 22.4 | 25 | |
| 21.7 | 2 | |
| 20.3 | 9 | |
| 18.6 | 33 | |
| 17.6 | 29 | |
| 17.5 | 31 | |
| 17.3 | 11 | |
| 14.2 | 7 | horn* |
| 12.6 | 14 | |
| 10.3 | 18 | |
| 9.7 | 12 | reef-building |

(Johnson *et al.,* 1995), which is consistent with the high diversity of molluscan faunas in Recent, Caribbean seagrass environments (Jackson, 1972, 1973). In contrast, abundant deep burrows were absent from most horizons where corals were common (Appendix B, this volume). The implications of this very preliminary analysis are that comparatively stable sediments, as inferred from the abundance of corals and absence of deep burrows, supported higher molluscan diversity than unstable sediments, just as in the Recent.

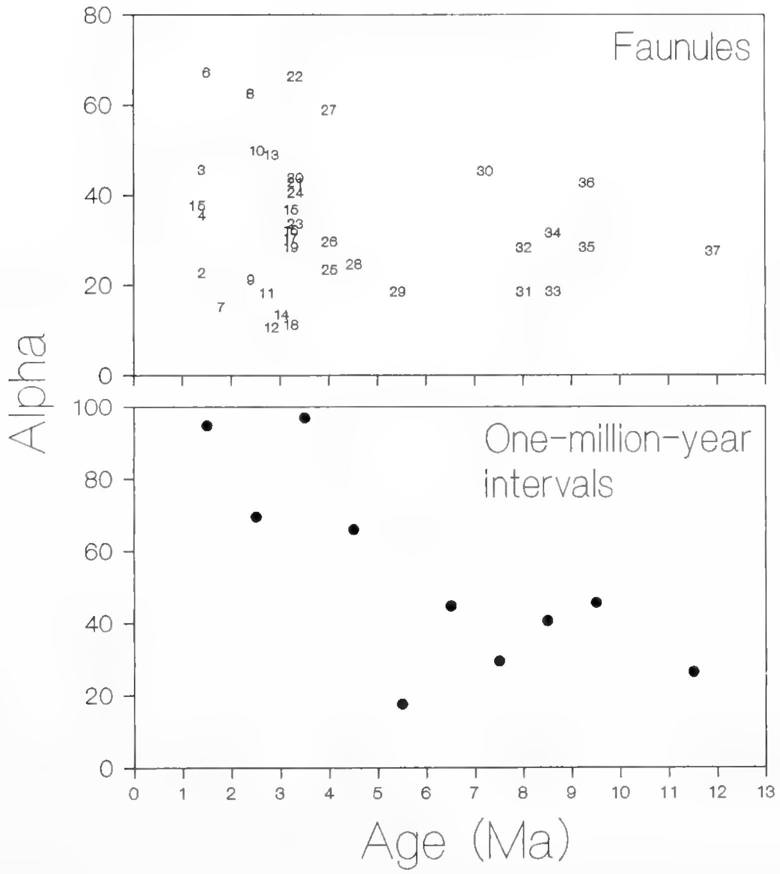
In spite of all this environmental heterogeneity, there is no significant change in alpha of the 37 faunules over the 10.2 million years for which we have collections (Text-fig. 14, top; Spearman rank-order correlation, $r = -0.138$, $P = 0.415$). This apparent stability strongly supports an earlier conclusion that southern Caribbean molluscan diversity did not decline during the past 12 million years (Jackson *et al.,* 1993; Jackson, 1994) despite faunal turnover at the end of the Pliocene. Moreover, alpha increases significantly towards the Recent using the data for one-million-year intervals (Text-fig. 14, bottom; Spearman rank order correlation, $r = -0.751$, $P = 0.012$). This result is obviously biased by the much greater number of faunules in the younger intervals, and thus the much greater variety of environments sampled. Regardless, diversity definitely did not decrease as had been claimed previously (Woodring, 1966; Stanley, 1986; Vermeij and Petuch, 1986).

## ORDINATION OF FAUNULES

We used detrended correspondence analysis (DCA) as a measure of similarities in molluscan faunal composition of the 37 faunules based on the occurrence of common taxa. To examine possible trends in faunal composition, we calculated Spearman rank-order correlations between scores on the DCA axes and the ages and paleodepths of each faunule as presented in Table 2. DCA is a non-parametric procedure analogous to principal components analysis in relating differences in generic or subgeneric occurrences to independent axes of decreasing variation by the eigenanalysis of a matrix of chi-square distances between collections (McCune and Medford, 1995). To calculate the ordinations, we used the DCA option of the PC-ORD program (*ibid.*).

The ordinations were repeated using both binary (presence-absence) and ranked abundance data for the occurrence of the 25 most abundant molluscan genera or subgenera in each of the 37 faunules (Appendix 3). When there were ties in the abundance of the 25th most abundant genus or subgenus in a faunule, we included all of the taxa that were tied. In these cases the numbers of genera or subgenera in a faunule is greater than 25. We used ranked abundance (0 specimens = 0, 1–9 specimens = 1, 10–99 specimens = 2, 100–999 specimens = 3, ≥ 1000 specimens = 4) rather than raw abundance because the latter is more sensitive to sampling bias.

The choice of the 25 commonest taxa from each faunule resulted in lists of 254 unique molluscan genera or subgenera. Eleven of the 156 genera or subgenera represented by >100 specimens (Text-fig. 12, App. 2) are not included among the 254 unique mollusk taxa in Appendix 3 because they were not among the top 25 taxa in any faunule. In contrast, 109 genera and subgenera among the 256 unique mollusks are represented by fewer than 100 specimens in all of the collections combined. These are listed in order of numerical abun-



Text-figure 14.—Variation in Fisher's diversity index alpha with age for all mollusks in the 37 faunules listed in Table 3 and for the one-million year intervals in Text-figures 6–7.

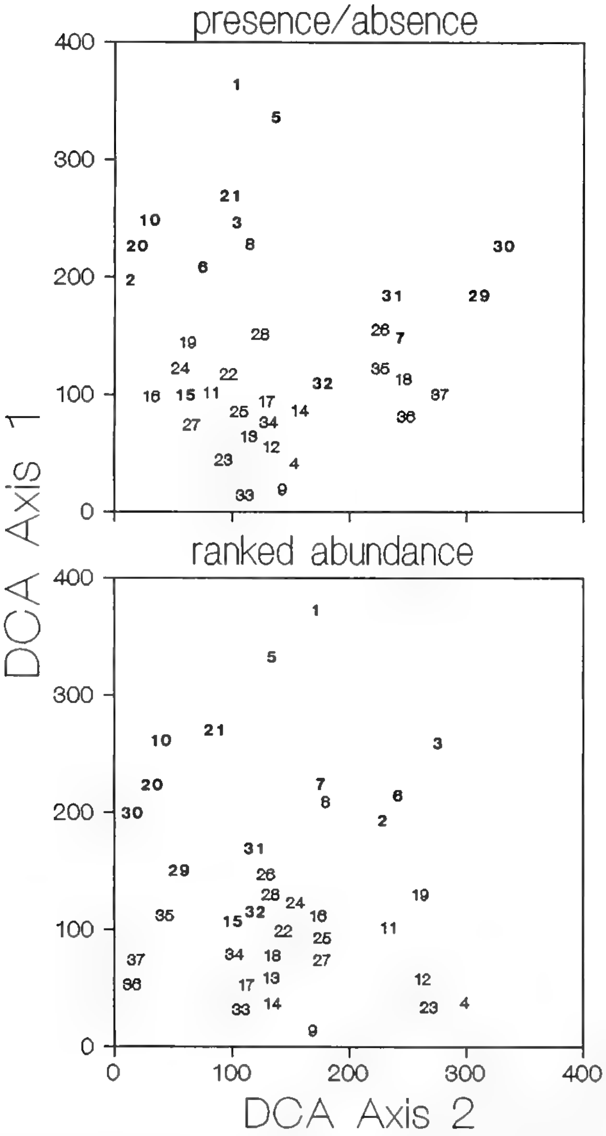
dance at the end of Appendix 2. Each of these 109 taxa occurs in very few faunules where, however, they are relatively abundant. Thus it should be possible to discriminate faunules dominated by otherwise rare taxa that would be excluded from any list based solely on total abundance for all the collections combined.

Results of the DCA analyses are illustrated separately for binary and ranked abundance data in Text-figure 15. Simple inspection suggests that faunule composition strongly varies with age and depth along the ordination axes 2 and 1 respectively. Moreover, the separation of faunules by age along axis 2 is clearer for the analysis using ranked abundance data than for binary data. These impressions are confirmed by highly significant correlations of the ordination scores on axis 2 with age ($r = -0.623$, $P < 0.001$) and of the scores on axis 1 with depth ($r = 0.740$, $P < 0.001$) for analyses based on ranked abundances (Text-fig. 16). In contrast, correlations of scores on axis 2 with age were only marginally significant ($r = 0.380$, $P = 0.020$) for analyses based on binary data, but were significant for scores on axis 1 with depth ($r = 0.688$, $P < 0.001$).

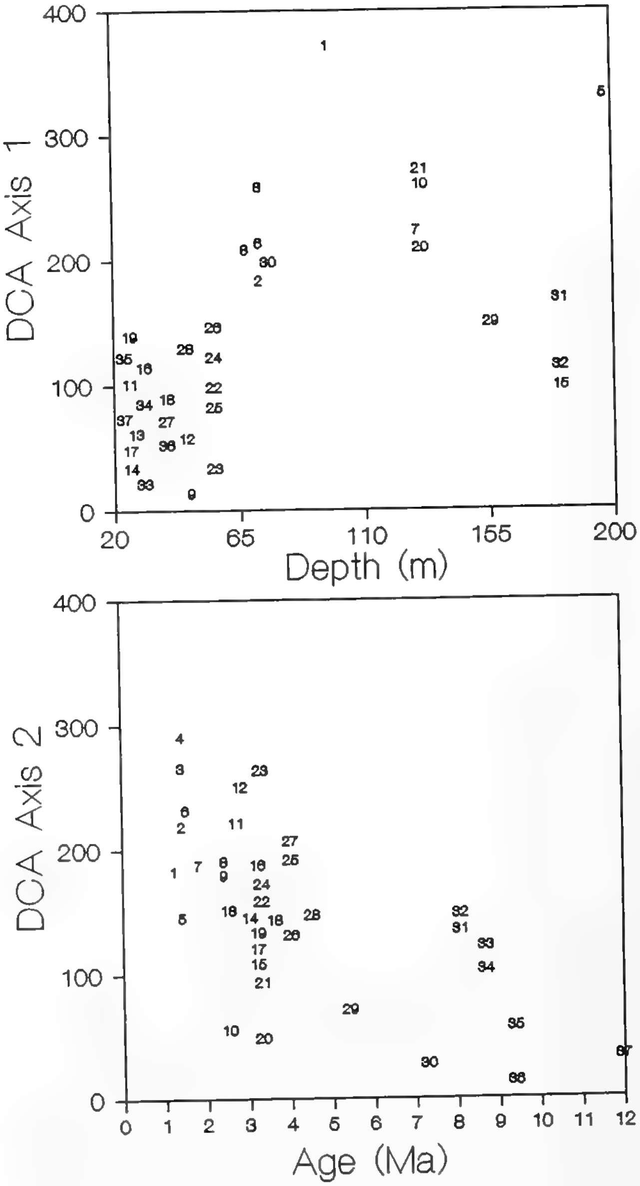
These results appear to support the use of ranked abundances rather than simple binary data in paleoecological analyses and studies of macroevolutionary trends (Jackson and McKinney, 1990). However, the number of faunules is not great. Thus, as the number of faunules increases, differences between the results of ordination analyses based on binary and ranked abundance data are likely to decrease (Hayek and Buzas, 1997).

## DISCUSSION

The diversity of our collections exceeds that of all previous studies of Caribbean Neogene mollusks (compare Table 1 and Text-fig. 8). Numbers of genera or subgenera in our collections from one-million-year intervals of the Late Pliocene exceed those for any other Neogene Caribbean collection. In addition, numbers of taxa for all but two of the remaining one-million-year intervals sampled equals or exceeds that of the faunas listed in Table 1 except for the Bowden and middle Gatun formations. Similar claims can be made for about half of the 37 faunules in Table 3. Nevertheless, our collections are still subject to sampling biases in age, environment and geography (Text-figs. 6–11, 13). Some of these problems should be at least



Text-figure 15.—Plots of detrended correspondence analyses (DCA) for the 37 faunules listed by the same numbers as in Table 3. Numbers increase from youngest (1) to oldest (37). Faunules from estimated water depths > 75 m indicated in boldface. Data for the ordinations are occurrences (presence-absence or ranked abundance) of the 254 molluscan genera or subgenera listed in Appendix 3.



Text-figure 16.—DCA axis scores versus age and depth of water for the 37 molluscan faunules as numbered in Table 3. Data for the ordination analyses were ranked abundances of the 254 genera or subgenera listed in Appendix 3.

partially resolved when we incorporate extensive new collections from the same three sedimentary basins, and from the transisthmian Chuqunaque Basin in Darien, that are now being processed.

The differences in numbers of taxa between PPP and earlier collections reflect greater collecting effort, and are not unique to the three basins sampled. For example, Jung's (1965) description of the early Middle Miocene Cantaure Formation was based on oil company reconnaissance collections that produced 109 genera and subgenera and 146 species. In contrast, repeated collecting over more than ten years by Jack and Winifred Gibson-Smith from the same localities at Cantaure produced 471 genera and subgenera and 737 species now at the Naturhistorisches Museum in Basel (unpubl. PPP-NMB taxonomic database compiled by Felix Wiedenmayer). Likewise, published faunas from the Mare Formation (Weisbord, 1962, 1964) include 164 genera and subgenera and 226 species, versus 352 genera and subgenera and 531 species in the Gibson-Smith collections (*ibid.*).

Despite all these caveats about sampling, a number of apparently robust patterns have emerged. Slopes of the cumulative diversity curves for different ages and basins (Text-fig. 8) appear to be stable with the repeated addition of new collections. This suggests that the slopes of the cumulative curves can be used reliably to infer the comparative diversity of our faunas, much like Fisher's diversity index alpha (Fisher *et al.*, 1943; Magurran, 1988; Hayek and Buzas, 1997). In addition, the list of the most abundant taxa in our collections (Apenidx 2) is unlikely to change much with further collecting, except for reasons of taxonomic refinement, because most taxa are extremely rare (Text-fig. 11).

Most of the abundant genera and subgenera have very long stratigraphic ranges in our collections (Appendix 2), which suggests that they were eurytopic. Restriction of a minority of abundant taxa to relatively few collections (Text-fig. 12) may be due to rapid evolutionary turnover or stenotopy (Jackson, 1974), or to environmental or stratigraphic biases in our collections. In addition, difficulty of collection (*e.g.*, large, fragile bivalves) and diagenesis (Koch and Sohl, 1983) may be important factors. For example, shells are typically leached and the matrix sandy at all the collection sites in the Gatun and Rio Banano formations. Lastly, large, attractive, or rare taxa, such as many of the turrid gastropods, inevitably attract more attention in the field, and are therefore likely to be over-represented relative to their actual frequency of occurrence.

Molluscan diversity generally increases while abundance generally decreases with increasing depth in Recent seas (Sanders, 1968, 1969; Jackson, 1972, 1974; Rex, 1981). Abundance of fossils per volume of sediment also decreases dramatically with depth in our collections (Table 3). Abundance is especially low at outcrops of deep continental shelf to continental slope deposits including Cangrejos Creek, Bruno Bluff, Shark Hole Point, and Rio Sand Box. Moreover, faunules from other deeper water horizons, such as the Nancy Point Formation (Coates *et al.*, 1992; Coates, this volume), could not be included in the ordination analyses because the collections were too small. Sediments deposited in water depths ≥150 m are therefore very difficult to sample, and estimates of diversity are accordingly uncertain compared to more fossiliferous deposits. Much more collecting is required to determine whether diversity increases with depth as in the Recent.

The apparent stability or increase of molluscan diversity in the southern Caribbean over ten million years (Text-fig. 14) is consistent with data for Pliocene to Recent molluscan diversity in Florida (Allmon *et al.*, 1993, 1996). Both of these results contrast with the abrupt decline in diversity of the *Strombina*-group and other so-called paciphile mollusks in the Late Pliocene about 2–3 Ma. (Woodring, 1966; Vermeij, 1978; Jung, 1989; Jackson *et al.*, 1993, 1996). Total Caribbean reef coral diversity also declined precipitously at the end of the Pliocene despite an extended burst of origination throughout most of the Late Pliocene (Budd *et al.*, 1996; Budd and Johnson, 1997).

The ordination analyses effectively discriminate among faunules based on age and water depth. Differences in the composition of faunules separated by only 100 m of depth may be as great as differences among faunules separated by ten million years. Similarly, large differences in faunal composition between water depths have been reported for ostracodes from the continental slope versus the deep sea ranging in age from Cretaceous to Pleistocene (Benson, 1979). Much more detailed analyses of sedimentary facies of the different faunules are required to understand the environmental basis of faunal variation.

## SUMMARY

Our study is the largest yet attempted to describe molluscan diversity and faunal composition from the Neogene of tropical America. Problems of sampling have been largely overcome, although older collections are limited to a few, exclusively very shallow-water deposits. Local diversity at the level of the faunule varies more than six-fold, and is generally highest where corals (and perhaps seagrasses) were present. As in Recent seas, molluscan abundance decreases greatly with depth. In contrast, diversity does not increase with depth as in the Recent, most probably because of problems of finding enough fossils in deeper water deposits. Diversity as estimated by Fisher's alpha was constant, or may even have increased, over the ten million years studied. This stability clearly lays to rest the earlier view of mass extinction and decreased diversity after the Early Pliocene. Ordination using DCA separates faunules along axes highly significantly correlated with age and depth, which provides a good first step towards separating the evolutionary and ecological bases for changes observed.

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## APPENDIX 1

### AGES AND PALEOBATHYMETRIES OF FAUNULES

These are ages and paleobathymetries for the 37 faunules in Table 2. Ages were provided by A. G. Coates (written commun., 1998; see also Aubry and Berggren in Coates this volume; Bybell, this volume; Cotton, this volume; McNeill *et al.*, in press). Most water depths are based on analyses of benthic foraminifera (Laurel Collins, written communs., 1996, 1998; Collins, 1993; Collins *et al.*, 1995; Collins *et al.*, 1996). Exceptions indicated by footnotes were based on stratigraphic relationships. Section numbers of Appendix B, this volume.

| Faunule (with section #) | Age (Ma) | Depth (m) | Abundant diagnostic taxa |
|---|---|---|---|
| 1. Swan Cay (#25) | 1.6–1.2 | 80–120[1] | *Amphistegina gibbosa, Cassidulina curvata, Eponides antillarum, Eponides repandus, Pararotalia rosea, Planulina ariminensis* var. *exorna, Quinqueloculina lamarckiana, Siphonina pulchra* |
| 2. Cemetery Pueblo Nuevo (#35) | 1.7–1.5 | 50–100 | based on lithostratigraphic relation to faunule #3 |
| 3. Upper Lomas del Mar East (reef) (#36) | 1.7–1.5 | 50–100 | *C. curvata, Elphidium discoidale, P. ariminensis* var. *exorna, Sigmoilina tenuis, Spirillina vivipara* |
| 4. Empalme (#34) | 1.7–1.5 | 10–30 | *E. discoidale, Fursenkoina pontoni, Nonionella atlantica, Pararotalia magdalenensis, Sagrina pulchella* |
| 5. Cangrejos Creek (#37) | 1.6–1.5 | 150–250 | *Bulimina aculeata, Bulimina marginata, Cassidulina minuta, Gyroidina regularis, Planulina foveolata, Trifarina eximia* |
| 6. Lomas del Mar East (non-reef) (#36) | 1.9–1.5 | 50–100 | based on lithostratigraphic relation to Faunule #3 |
| 7. Northwest Escudo de Veraguas (#10) | 2.1–1.9 | 100–150 | *Bolivina paula, B. marginata, C. curvata, C minuta, G. regularis, Hanzawaia concentrica, Melonis barleeanum, Reussella spinulosa, S. tenuis, S. pulchra, Uvigerina laevis, Uvigerina peregrina* |
| 8. Fish Hole (#22/23) | 3.0 2.2 | 75–100 (upper mudstone)<br>40–100 (lower reef conglomerate) | *B. marginata, E. antillarum, P. ariminensis* var. *exorna, T. eximia, U. peregrina, A. gibbosa, E. discoidale, E. antillarum, Nodobaculariella cassis, P. ariminensis* var. *exorna, Q. lamarckiana, S. pulchra* |
| 9. Ground Creek (no section) | 3.5–1.6[3] | <50? | estimate based on sediments and mollusks |
| 10. North-central Escudo de Veraguas (#10) | 3.6–1.9 | 100–150 | same as Faunule #7 |
| 11. Rio Limoncito (no section) | 3.6–2.4 | 20–40? | based on apparent stratigraphic relationship to Faunule #'s 13 and 17–19 |
| 12. Chocolate Buenos Aires (#33) | 3.2–3.0 | <50? | Based on lithostratigraphic position between reef trends |
| 13. Bomba (#29) | 3.2–2.9 | 20–40 | *Ammonia decorata, P. magdalenensis, P. sarmientoi, Rotorbinella umbonata, S. tenuis* |
| 14. Agua (#29) | 3.6–2.9 | 20–40 | Based on stratigraphic relations to Faunule #'s 13, 17–19 |
| 15. Bruno Bluff (#12) | 3.6–3.3 | 150–200 | *B. marginata, C. curvata, C. minuta, C. norcrossi australis, T. eximia, U. peregrina* |
| 16. Cayo Agua: West side of Punta Norte (#16) | 3.5 | 20–40 | *E. discoidale, E. antillarum, F. pontoni, H. concentrica, N. cassis, N. atlantica, Quinqueloculina compta, Q. lamarckiana* |
| 17. Quiteria (#29) | 3.6–3.4 | 20–40 | Same as Faunule #'s 13 and 19 |
| 18. Rio Vizcaya (#39) | 3.5 | <25 | *Ammonia beccarii, A. gibbosa, Buccella hannai, N. atlantica, P. magdalenensis, Trifarina occidentalis* |
| 19. Santa Rita (#32) | 3.5 | 20–40 | *A. gibbosa, E. antillarum, Hauerina fragillissima, N. cassis, P. ariminensis* var. *exorna, R. umbonata* |
| 20. Northeast Escudo de Veraguas (#10) | 3.6–3.5 | 100–150 | Same as Faunule #7 |
| 21. Southeast Escudo de Veraguas (#11) | 3.6–3.5 | 100–150 | Same as Faunule #7 |
| 22. Cayo Agua: Punta Tiburon (#19) | 3.6–3.5 | 40–80 | *Cassidulina subglobosa, E. discoidale, E. antillarum, F. pontoni, H. concentrica, N. atlantica, P. ariminensis, R. spinulosa, S. tenuis* |
| 23. Cayo Agua: Punta Nispero West (#19) | 3.6–3.5 | 40–80 | Same as Faunule #22 |
| 24. Cayo Agua: Punta Nispero Southeast (#20) | 3.6–3.5 | 40–80 | Same as Faunule #22 |
| 25. Isla Popa (no section) | 5.0–3.5 | <50? | Based on apparent stratigraphic equivalence and proximity to older Cayo Agua Fm. |
| 26. Cayo Agua: Punta Norte East (#19) | 5.0–3.5 | 40–80 | Same as Faunule #22 |

APPENDIX 1.—Continued.

| Faunule (with section #) | Age (Ma) | Depth (m) | Abundant diagnostic taxa |
|---|---|---|---|
| 27. Cayo Agua: Punta Piedra Roja West (#17) | 5.0–3.5 | 10–75 | *A. gibbosa, Cancris sagra, E. discoidale, E. antillarum, Quinqueloculina* spp. |
| 28. Quebrada Brazo Seco (no section) | 5.2–4.3 | <50? | Based on stratigraphic position between reef tracts and Rio Banano Fm. |
| 29. Shark Hole Point and top of Nancy Point (#12) | 5.7–5.6 | 100–200 | *Bolivina barbata, Bolivina imporcata, N. atlantica, P. ariminensis, U. peregrina* |
| 30. Finger Island (#14) | 8.2–5.6 | 60–100 | *A. gibbosa, B. barbata, C. curvata, E. antillarum, H. concentrica, Hanzawaia isidroensa, Lenticulina calcar, P. ariminensis, Quinqueloculina seminulum, S. pulchra, U. peregrina* |
| 31. Rio Sand Box (#27) | 8.7–7.2 | 150–200 | *B. imporcata, Bolivina lowmani, Bolivina mexicana, C. minuta, N. atlantica, P. magdalenensis, R. umbonata* |
| 32. Rio Tuba (no section) | 8.2–7.2[4] | 150–200 | Assumed equivalent to Faunule #31 based on apparent stratigraphic position |
| 33. Rio Calzones (#9) | 11.2–5.3[5] | 25? | assumed equivalent to Faunule #34 |
| 34. Miguel de la Borda (#6) | 11.2–5.3[5] | 25? | |
| 35. Isla Payardi (#1) | 9.4–8.6 | 15–40 | *A. beccarii, Bolivina merecuani, Bolivina vaughani, B. hannai, P. magdalenensis, R. spinulosa, R. umbonata* |
| 36. Mattress Factory (#1) | 9.4–8.6 | 15–40 | same as Faunule #35 |
| 37. Martin Luther King (#1) | 11.8–11.4[6] | 15–40 | same as Faunule #35 |

[1] We used the maximum rather than the median depth because the sediments are a reef talus slump deposit.

[2] Assumed Late Pliocene age based on inferred stratigraphic position.

[3] Assumed equivalent to older Cayo Agua Fm.

[4] Assumed equivalent to nearby Rio Sandbox.

[5] Assumed Late Miocene (Collins *et al.*, 1996).

## APPENDIX 2

### COMMON GENERA OR SUBGENERA

Taxa are listed in order of abundance by total number of specimens in all collections combined. The list includes all 156 taxa represented by ≥100 specimens, plus all 109 additional taxa included among the top 25 taxa for each of the 37 faunules listed in Appendix 3. Numbered taxonomic notes concern common problematic taxa. An asterisk (*) indicates an informal designation or loosely applied name for a presently poorly resolved group requiring further study.

| Genus and subgenus | Family | Class | Number of specimens | Cumulative number of specimens | Number of collections | Number of faunules | Used in ordinations | First occurrence (Ma) | Last occurrence (Ma) |
|---|---|---|---|---|---|---|---|---|---|
| *Turritella*[1] | Turritellidae | G | 10296 | 10296 | 152 | 30 | X | 11.6 | 1.4 |
| *Crassinella* Guppy | Crassatellidae | B | 5727 | 16023 | 114 | 29 | X | 11.6 | 1.4 |
| *Caryocorbula* Gardner | Corbulidae | B | 5310 | 21333 | 126 | 30 | X | 11.6 | 1.6 |
| *Varicorbula* Grant & Gale | Corbulidae | B | 5206 | 26539 | 87 | 27 | X | 9.6 | 1.4 |
| *Olivella* (*Dactylidella*) Woodring | Olividae | G | 4816 | 31355 | 32 | 10 | X | 4.8 | 1.7 |
| *Anadara* (*Rasia*) Gray | Arcidae | B | 3415 | 34770 | 150 | 33 | X | 11.6 | 1.4 |
| *Cymatophos* Pilsbry & Olsson | Buccinidae | G | 3133 | 37903 | 34 | 7 | X | 11.6 | 1.7 |
| *Tucetona* Iredale | Glycymerididae | B | 2759 | 40662 | 106 | 30 | X | 9.6 | 1.4 |
| *Alabina* Dall | 'Obtortionidae' | G | 2641 | 43303 | 114 | 24 | X | 11.6 | 1.4 |
| *Nassarius* (s.l.)[2] Duméril | Nassaridae | G | 2570 | 45873 | 118 | 33 | X | 11.6 | 1.4 |
| *Conus*[3] Linnaeus | Conidae | G | 2313 | 48186 | 175 | 35 | X | 11.6 | 1.4 |
| *Strioterebrum* Sacco | Terebridae | G | 2135 | 50321 | 129 | 30 | X | 11.6 | 1.4 |
| *Cadulus*[4] | Gadilidae | S | 2109 | 52430 | 108 | 31 | X | 11.6 | 1.4 |
| *Ervilia* Turton | Semelidae | B | 2013 | 54443 | 32 | 8 | X | 11.6 | 3.1 |
| *Antillophos* (*Antillophos*) Woodring | Buccinidae | G | 1989 | 56432 | 90 | 24 | X | 11.6 | 1.4 |
| *Argopecten* Monterosato | Pectinidae | B | 1894 | 58326 | 105 | 27 | X | 9.6 | 1.4 |
| *Oliva* (*Oliva*) Bruguière | Olividae | G | 1867 | 60193 | 153 | 34 | X | 11.6 | 1.4 |
| *Anadara* (*Cunearca*)[5] Dall | Arcidae | B | 1787 | 61980 | 50 | 11 | X | 11.6 | 1.6 |
| *Olivella* (*Olivella*) Swainson | Olividae | G | 1468 | 63448 | 39 | 17 | X | 9.6 | 2.6 |
| *Polinices* Montfort | Naticidae | G | 1396 | 64844 | 117 | 31 | X | 11.6 | 1.6 |
| *Cancellaria* (s.l.)[6] Lamarck | Cancellariidae | G | 1374 | 66218 | 96 | 22 | X | 11.6 | 1.6 |
| *Olivella* (*Niteoliva*) Olsson | Olividae | G | 1315 | 68848 | 41 | 12 | X | 11.6 | 1.6 |
| *Stigmaulax* Mörch | Naticidae | G | 1315 | 67533 | 114 | 29 | X | 11.6 | 1.6 |
| *Lirophora*[7] | Veneridae | B | 1314 | 70162 | 72 | 21 | X | 9.6 | 1.6 |
| *Natica* (*Naticarius*) Duméril | Naticidae | G | 1265 | 71427 | 96 | 28 | X | 11.6 | 1.6 |
| *Strombina* (*Strombina*) Mörch | Columbellidae | G | 1204 | 72631 | 30 | 3 | X | 11.6 | 9.6 |
| *Volvarina* Hinds | Marginellidae | G | 1183 | 73814 | 96 | 28 | X | 9.6 | 1.4 |
| *Acteocina* Gray | Cylichnidae | G | 1167 | 74981 | 100 | 27 | X | 11.6 | 1.6 |
| caecid[8] | Caecidae | G | 1161 | 76142 | 83 | 28 | X | 11.6 | 1.6 |
| *Parvilucina* (s.l.) Dall | Lucinidae | B | 1111 | 77253 | 88 | 28 | X | 9.6 | 1.4 |
| *Saccella* Woodring | Nuculanidae | B | 1106 | 78359 | 109 | 33 | X | 11.6 | 1.4 |
| *Polystira* Woodring | Turridae | G | 1104 | 79463 | 134 | 33 | X | 11.6 | 1.4 |
| *Sincola* (*Sincola*) Olsson & Harbison | Columbellidae | G | 1085 | 80548 | 34 | 11 | X | 11.6 | 3.1 |
| *Macrocallista* (*Megapitaria*) Grant & Gale | Veneridae | B | 1021 | 81569 | 79 | 22 | X | 11.6 | 1.6 |
| *Olivella* (*Minioliva*) Olsson | Olividae | G | 990 | 82559 | 43 | 15 | X | 11.6 | 1.4 |
| *Dentalium* (s.l.)[9] | Dentaliidae | S | 907 | 83466 | 105 | 30 | X | 11.6 | 1.4 |
| *Architectonica* Röding | Architectonicidae | G | 902 | 84368 | 119 | 31 | X | 11.6 | 1.6 |
| *Prunum* Herrmansen | Marginellidae | G | 892 | 85260 | 99 | 27 | X | 9.6 | 1.6 |
| *Trigoniocardia* (s.l.)[10] Dall | Cardiidae | B | 885 | 86145 | 78 | 23 | X | 11.6 | 1.6 |
| *Olivella* (*Macgintiella*) Olsson | Olividae | G | 868 | 87013 | 64 | 20 | X | 7.7 | 1.4 |
| *Persicula* Schumacher | Marginellidae | G | 839 | 87852 | 49 | 16 | X | 11.6 | 1.4 |

APPENDIX 2.—Continued.

| Genus and subgenus | Family | Class | Number of specimens | Cumulative number of specimens | Number of collections | Number of faunules | Used in ordinations | First occurrence (Ma) | Last occurrence (Ma) |
|---|---|---|---|---|---|---|---|---|---|
| *Strombus*[11] Linnaeus | Strombidae | G | 839 | 88691 | 110 | 27 | X | 9.6 | 1.6 |
| *Gouldia* C.B. Adams | Veneridae | B | 722 | 89413 | 61 | 23 | X | 8.6 | 1.4 |
| *Siliquaria* Bruguière | Siliquariidae | G | 698 | 90111 | 22 | 6 | X | 3.6 | 1.4 |
| turbonilline[12] | Pyramidellidae | G | 692 | 90803 | 118 | 30 | X | 11.6 | 1.4 |
| *Voluta* Linnaeus | Volutidae | G | 688 | 91491 | 101 | 29 | X | 8.6 | 1.4 |
| *Ringicula (Ringiculella)* Sacco | Ringiculidae | G | 647 | 92138 | 81 | 22 | X | 9.6 | 1.4 |
| *Chama* Linnaeus | Chamidae | B | 627 | 92765 | 72 | 23 | X | 9.6 | 1.4 |
| *Hyotissa* Stenzel | Gryphaeidae | B | 603 | 93368 | 47 | 14 | X | 11.6 | 1.4 |
| *Agladrillia (Agladrillia)* Woodring | Turridae | G | 551 | 93919 | 67 | 21 | X | 11.6 | 1.4 |
| *Chione* Megerle | Veneridae | B | 539 | 94458 | 21 | 11 | X | 11.6 | 1.6 |
| *Alveinus* Conrad | Kelliellidae | B | 522 | 94980 | 16 | 3 | X | 11.6 | 3.6 |
| *Nucula (Nucula)* Lamarck | Nuculidae | B | 491 | 95471 | 27 | 14 | X | 8.6 | 2.6 |
| *Cylichnella* Gabb | Cylichnidae | G | 487 | 95958 | 52 | 15 | X | 11.6 | 1.7 |
| *Leptopecten* Verrill | Pectinidae | B | 478 | 96436 | 39 | 11 | X | 11.6 | 2.6 |
| *Gadilopsis* Woodring | Gadilidae | S | 435 | 96871 | 11 | 6 | X | 9.6 | 2.8 |
| *Petaloconchus* Lea | Vermetidae | G | 433 | 97304 | 49 | 18 | X | 11.6 | 1.6 |
| *Dentimargo* Cossmann | Marginellidae | G | 433 | 97737 | 38 | 13 | X | 7.7 | 1.7 |
| *Cyclopecten* Verrill | Propeamussiidae | B | 424 | 98161 | 64 | 24 | X | 11.6 | 1.6 |
| *Mitra*[13] Lamarck | Mitridae | G | 417 | 98578 | 19 | 9 | X | 9.6 | 1.6 |
| *Volvulella (Volvulella)* Newton | Retusidae | G | 407 | 99392 | 95 | 30 | X | 11.6 | 1.4 |
| *Sulcoretusa* Burch | Retusidae | G | 407 | 98985 | 79 | 25 | X | 9.6 | 1.4 |
| scaphopod* |  | S | 392 | 99784 | 41 | 14 | X | 9.6 | 1.6 |
| *Anadara (Potiarca)* Iredale | Arcidae | B | 382 | 100166 | 15 | 7 | X | 9.6 | 3.1 |
| rissoine[14] | Rissoidae | G | 374 | 100540 | 46 | 16 | X | 7.7 | 1.4 |
| *Crenella* Brown | Mytilidae | B | 371 | 100911 | 67 | 21 | X | 11.6 | 1.4 |
| *Chionopsis* Olsson | Veneridae | B | 368 | 101279 | 50 | 12 | X | 11.6 | 1.6 |
| *Haustellum* Schumacher | Muricidae | G | 359 | 101638 | 79 | 19 | X | 11.6 | 1.4 |
| *Volvarina* ? Hinds | Marginellidae | G | 353 | 101991 | 15 | 8 | X | 7.7 | 1.6 |
| turrid* | Turridae | G | 341 | 102332 | 62 | 22 | X | 9.6 | 1.4 |
| *Crucibulum (Crucibulum)* Schumacher | Calyptraeidae | G | 340 | 102672 | 77 | 23 | X | 11.6 | 1.6 |
| *Luria* Jousseaume | Cypraeidae | G | 332 | 103004 | 10 | 4 | X | 1.7 | 1.4 |
| *Cavolinia* Abildgaard | Cuvierinidae | G | 328 | 103332 | 48 | 12 | X | 4.3 | 1.6 |
| pyramidelline[15] | Pyramidellidae | G | 324 | 103656 | 71 | 21 | X | 11.6 | 1.6 |
| *Dimya* Rouault | Dimyidae | B | 322 | 103978 | 22 | 7 | X | 3.5 | 1.4 |
| *Serpulorbis* Sacco | Vermetidae | G | 310 | 104288 | 48 | 17 | X | 9.6 | 1.4 |
| *Bulla* Linnaeus | Bullidae | G | 304 | 104592 | 14 | 7 | X | 4.3 | 1.6 |
| *Hindsiclava* Hertlein & Strong | Turridae | G | 299 | 104891 | 74 | 21 | X | 11.6 | 1.4 |
| *Solenosteira* Dall | Buccinidae | G | 276 | 105167 | 49 | 14 | X | 11.6 | 2.6 |
| eulimid[16] | Eulimidae | G | 275 | 105442 | 80 | 27 | X | 11.6 | 1.4 |
| *Axinactis (Glycymerella)* Woodring | Glycymerididae | B | 261 | 105703 | 41 | 19 | X | 9.6 | 1.6 |
| *Nucula (Lamellinucula)* Schenck | Nuculidae | B | 244 | 105947 | 47 | 14 | X | 4.3 | 1.6 |
| *Sconsia* Gray | Cassidae | G | 242 | 106189 | 55 | 19 | X | 7.7 | 1.6 |
| *Flabellipecten* Sacco | Pectinidae | B | 240 | 106429 | 48 | 18 | X | 11.6 | 1.6 |
| *Limacina* Bosc | Limacinidae | G | 240 | 106669 | 33 | 13 | X | 9.6 | 1.6 |
| *Clathrodrillia*[17] | Turridae | G | 239 | 106908 | 67 | 20 |  | 11.6 | 1.4 |

APPENDIX 2.—Continued.

| Genus and subgenus | Family | Class | Number of specimens | Cumulative number of specimens | Number of collections | Number of faunules | Used in ordinations | First occurrence (Ma) | Last occurrence (Ma) |
|---|---|---|---|---|---|---|---|---|---|
| *Calyptraea* Lamarck | Calyptraeidae | G | 231 | 107139 | 35 | 14 | X | 11.6 | 1.6 |
| *Teinostoma*[18] H. & A. Adams | Adeorbidae | G | 231 | 107370 | 67 | 25 | X | 11.6 | 1.4 |
| *Niso* Risso | Eulimidae | G | 229 | 107599 | 60 | 21 | X | 11.6 | 1.6 |
| *Kelliella* M. Sars | Kelliellidae | B | 223 | 107822 | 9 | 4 | X | 3.6 | 2.8 |
| *Meioceras* Carpenter | Caecidae | G | 222 | 108044 | 26 | 12 | X | 8.6 | 2.6 |
| typhine[19] | Muricidae | G | 221 | 108265 | 62 | 22 | X | 11.6 | 1.4 |
| *Plicatula* Lamarck | Plicatulidae | B | 211 | 108476 | 34 | 11 | X | 4.3 | 1.6 |
| carditesine[20] | Carditidae | B | 209 | 108685 | 38 | 16 | X | 11.6 | 1.4 |
| *Subcancilla* Olsson & Harbison | Mitridae | G | 209 | 108894 | 63 | 22 | X | 11.6 | 1.6 |
| *Alvania* Risso | Rissoidae | G | 207 | 109101 | 41 | 16 | X | 9.6 | 1.4 |
| *Styliola* Lessueur | Cuvierinidae | G | 204 | 109509 | 34 | 12 | X | 9.6 | 1.6 |
| *Fissidentalium* Fischer | Dentaliidae | S | 204 | 109305 | 18 | 8 | X | 7.7 | 1.6 |
| *Arcinella* Schumacher | Chamidae | B | 203 | 109712 | 48 | 14 | X | 11.6 | 2.8 |
| *Tellidorella* Berry | Cardiniidae ? | B | 202 | 109914 | 7 | 6 | X | 6.9 | 2.8 |
| *Eucrassatella* (*Hybolophus*) Stewart | Crassatellidae | B | 200 | 110114 | 21 | 6 | X | 11.6 | 3.1 |
| *Natica** | Naticidae | G | 192 | 110306 | 36 | 15 | X | 11.6 | 1.6 |
| *Crepidula* Lamarck | Calyptraeidae | G | 187 | 110493 | 38 | 11 | X | 11.6 | 3.1 |
| *Knefastia* Dall | Turridae | G | 184 | 110677 | 41 | 15 | X | 4.3 | 1.4 |
| *Moerella* Fischer | Tellinidae | B | 178 | 110855 | 10 | 5 | X | 9.6 | 3.5 |
| *Ithycythara* Woodring | Turridae | G | 176 | 111031 | 49 | 18 | X | 11.6 | 1.4 |
| *Marginella* Lamarck | Marginellidae | G | 176 | 111207 | 15 | 10 | X | 6.9 | 1.6 |
| *Granulina* Jousseaume | Marginellidae | G | 174 | 111381 | 15 | 6 | X | 3.5 | 1.4 |
| triphorid[21] | Triphoridae | G | 168 | 111549 | 34 | 17 | X | 9.6 | 1.4 |
| *Noetia** Gray | Noetiidae | B | 167 | 111716 | 29 | 9 | X | 11.6 | 3.0 |
| *Tesseracme* Pilsbry & Sharp | Dentaliidae | S | 164 | 112044 | 36 | 10 | X | 11.6 | 3.1 |
| *Dosinia* Scopoli | Veneridae | B | 164 | 111880 | 26 | 12 | X | 9.6 | 1.6 |
| *Vermicularia* Lamarck | Turritellidae | G | 162 | 112206 | 20 | 7 | X | 3.6 | 1.6 |
| *Limopsis* Sassi | Limopsidae | B | 161 | 112367 | 6 | 5 | X | 2.8 | 1.4 |
| *Kurtziella* (*Kurtziella*) Dall | Turridae | G | 160 | 112527 | 52 | 20 | X | 9.6 | 1.4 |
| *Cyclostremiscus* (*Ponocyclus*) Pilsbry | Skeneidae | G | 155 | 112682 | 38 | 16 | X | 11.6 | 1.4 |
| *Bathoxiphus* Pilsbry & Sharp | Entalinidae | S | 154 | 112836 | 20 | 9 | X | 8.6 | 2.8 |
| *Eulimella* (*Ebalina*) Thiele | Pyramidellidae | G | 151 | 112987 | 17 | 5 | X | 3.6 | 2.8 |
| *Barbatia* (*Barbatia*) Gray | Arcidae | B | 149 | 113136 | 24 | 8 | X | 4.3 | 1.6 |
| *Eupleura* H. & A. Adams | Muricidae | G | 147 | 113283 | 25 | 7 | X | 11.6 | 1.7 |
| *Anomia* Linnaeus | Anomiidae | B | 145 | 113718 | 31 | 13 | X | 9.6 | 1.6 |
| *Solariorbis*[22] Conrad | Adeorbidae | G | 145 | 113573 | 40 | 17 | X | 11.6 | 1.6 |
| *Diodora* Gray | Fissurellidae | G | 145 | 113428 | 22 | 6 | X | 3.5 | 1.4 |
| *Eurytellina* Fischer | Tellinidae | B | 142 | 113860 | 39 | 18 | X | 11.6 | 1.6 |
| *Trigonulina* d'Orbigny | Verticordiidae | B | 142 | 114002 | 44 | 14 | X | 6.9 | 1.6 |
| *Macrocypraea* Schilder | Cypraeidae | G | 138 | 114140 | 14 | 4 | X | 2.6 | 1.6 |
| *Terebra* (*Panaterebra*) Olsson | Terebridae | G | 136 | 114276 | 18 | 3 | X | 11.6 | 9.6 |
| *Metula* H. & A. Adams | Buccinidae | G | 129 | 114405 | 38 | 17 | X | 6.9 | 1.4 |
| *Distorsio* Röding | Personidae | G | 127 | 114532 | 46 | 16 |  | 11.6 | 1.4 |
| *Leionucula* Quenstedt | Nuculidae | B | 126 | 114658 | 31 | 13 | X | 3.6 | 1.4 |
| cardiid* | Cardiidae | B | 126 | 114784 | 15 | 7 |  | 11.6 | 3.1 |

APPENDIX 2.—Continued.

| Genus and subgenus | Family | Class | Number of specimens | Cumulative number of specimens | Number of collections | Number of faunules | Used in ordinations | First occurrence (Ma) | Last occurrence (Ma) |
|---|---|---|---|---|---|---|---|---|---|
| *Pectunculina* d'Orbigny | Limopsidae | B | 123 | 114907 | 8 | 3 | X | 9.6 | 2.8 |
| *Sincola* (*Sinaxila*) Jung | Columbellidae | G | 121 | 115028 | 13 | 7 | X | 4.8 | 2.1 |
| *Lucinisca* Dall | Lucinidae | B | 120 | 115148 | 24 | 14 | X | 9.6 | 1.6 |
| *Glyphostoma* (*Glyphostoma*) Gabb | Turridae | G | 119 | 115267 | 42 | 17 | X | 9.6 | 1.4 |
| *Latirus*[23] Montfort | Fasciolariidae | G | 119 | 115386 | 29 | 11 | X | 6.9 | 1.4 |
| *Malea* Valenciennes | Tonnidae | G | 117 | 115503 | 47 | 19 |  | 11.6 | 1.6 |
| *Carinodrillia* Dall | Turridae | G | 117 | 115620 | 47 | 23 | X | 9.6 | 1.4 |
| *Syntomodrillia* Woodring | Turridae | G | 117 | 115737 | 27 | 12 | X | 6.9 | 1.4 |
| *Bothrocorbula* (*Hexacorbula*) Olsson | Corbulidae | B | 116 | 115853 | 21 | 8 |  | 11.6 | 1.4 |
| *Marginella* ? Lamarck | Marginellidae | G | 116 | 115969 | 8 | 4 | X | 3.6 | 2.8 |
| *Myrtea* Turton | Lucinidae | B | 115 | 116084 | 11 | 7 | X | 9.6 | 1.7 |
| *Diacria* J.E. Gray | Cuvierinidae | G | 113 | 116197 | 19 | 8 | X | 4.3 | 1.6 |
| *Mitrella* Risso | Columbellidae | G | 112 | 116309 | 29 | 18 | X | 9.6 | 1.4 |
| *Abra* Leach | Semelidae | B | 111 | 116420 | 16 | 6 | X | 8.6 | 2.6 |
| *Bittium** Leach | Cerithiidae | G | 111 | 116531 | 11 | 5 |  | 11.6 | 3.6 |
| *Terebra* (*Oreoterebra*) Olsson | Terebridae | G | 109 | 116640 | 20 | 10 |  | 11.6 | 3.1 |
| *Laevidentalium* Cossmann | Laevidentaliidae | S | 106 | 116746 | 16 | 11 | X | 4.3 | 1.6 |
| *Microgaza* Dall | Trochidae | G | 105 | 116851 | 18 | 5 | X | 6.9 | 2.8 |
| *Strombina* (*Lirastrombina*) Jung | Columbellidae | G | 105 | 116956 | 19 | 7 |  | 5.7 | 3.1 |
| *Costoanachis* Sacco | Columbellidae | G | 104 | 117060 | 36 | 15 |  | 11.6 | 1.6 |
| *Pseudotorinia* Sacco | Architectonicidae | G | 102 | 117162 | 42 | 15 |  | 9.6 | 1.4 |
| *Mulinia* Gray | Mactridae | B | 101 | 117263 | 18 | 6 |  | 11.6 | 1.6 |
| *Arcopsis* von Koenen | Noetiidae | B | 101 | 117364 | 19 | 9 | X | 3.6 | 1.4 |
| *Calliostoma* Swainson | Trochidae | G | 100 | 117464 | 51 | 15 | X | 6.9 | 1.6 |
| *Tellina* (*Scissula*) Dall | Tellinidae | B | 100 | 117564 | 3 | 3 | X | 8.6 | 2.8 |
| *Eucrassatella* (*Eucrassatella*) Iredale | Crassatellidae | B | 98 | 117662 | 24 | 10 | X | 9.6 | 3.1 |
| *Eulimastoma* Bartsch | Pyramidellidae | G | 97 | 117759 | 39 | 18 | X | 9.6 | 1.6 |
| *Spondylus* Linnaeus | Spondylidae | B | 97 | 117856 | 28 | 10 | X | 8.6 | 1.4 |
| *Strombinophos* Pilsbry & Olsson | Columbellidae | G | 95 | 117951 | 39 | 12 | X | 9.6 | 1.6 |
| *Granula* Jousseaume | Marginellidae | G | 95 | 118046 | 4 | 4 | X | 3.6 | 1.4 |
| *Kurtziella* (*Cryoturris*) Woodring | Turridae | G | 88 | 118134 | 24 | 13 | X | 9.6 | 1.4 |
| *Semele* Schumacher | Semelidae | B | 88 | 118222 | 15 | 7 | X | 11.6 | 1.7 |
| *Sincola* (*Sinaxila*) ? Jung | Columbellidae | G | 87 | 118309 | 3 | 1 | X | 2.8 | 2.8 |
| *Crassostrea* Sacco | Ostreidae | B | 87 | 118396 | 2 | 2 | X | 11.6 | 1.6 |
| *Epitonium* (*Asperiscala*) Berry | Epitoniidae | G | 84 | 118480 | 27 | 14 | X | 11.6 | 1.6 |
| *Amarophos* Woodring | Buccinidae | G | 83 | 118563 | 7 | 2 | X | 7.7 | 5.7 |
| *Laevicardium* Swainson | Cardiidae | B | 83 | 118646 | 26 | 13 | X | 11.6 | 1.7 |
| *Fasciolaria* (*Fasciolaria*) Lamarck | Fasciolariidae | G | 83 | 118729 | 33 | 12 | X | 11.6 | 1.6 |
| *Trachycardium* (*Phlogocardia*) Stewart | Cardiidae | B | 83 | 118812 | 16 | 6 | X | 4.3 | 3.5 |
| *Yoldia* Moller | Yoldiidae | B | 82 | 118894 | 16 | 8 | X | 6.9 | 1.6 |
| naticid* | Naticidae | G | 82 | 118976 | 19 | 12 | X | 9.6 | 2.6 |
| *Zonaria* Jousseaume | Cypraeidae | G | 81 | 119057 | 10 | 3 | X | 1.7 | 1.6 |
| *Lamelliconcha* Dall | Veneridae | B | 80 | 119137 | 16 | 9 | X | 11.6 | 1.6 |
| *Coralliophila* H. & A. Adams | Coralliophilidae | G | 79 | 119216 | 12 | 5 | X | 4.3 | 1.4 |
| *Trachycardium* (s.l.)* Mörch | Cardiidae | B | 77 | 119293 | 22 | 15 | X | 11.6 | 1.6 |

APPENDIX 2.—Continued.

| Genus and subgenus | Family | Class | Number of specimens | Cumulative number of specimens | Number of collections | Number of faunules | Used in ordinations | First occurrence (Ma) | Last occurrence (Ma) |
|---|---|---|---|---|---|---|---|---|---|
| *Crassispira (Crassispira)* Swainson | Turridae | G | 74 | 119367 | 24 | 13 | X | 11.6 | 1.6 |
| *Compsodrillia* Woodring | Turridae | G | 72 | 119439 | 19 | 10 | X | 7.7 | 1.4 |
| *Neverita (Glossaulax)* Pilsbry | Naticidae | G | 71 | 119510 | 9 | 2 | X | 11.6 | 9.6 |
| *Natica (Natica)* Scopoli | Naticidae | G | 68 | 119578 | 11 | 7 | X | 9.6 | 1.4 |
| *Ostreola* Monterosato | Ostreidae | B | 65 | 119643 | 4 | 3 | X | 9.6 | 1.6 |
| *Lucinoma* ? Dall | Lucinidae | B | 65 | 119708 | 4 | 1 | X | 1.6 | 1.6 |
| *Jupiteria* Bellardi | Nuculanidae | B | 64 | 119772 | 18 | 9 | X | 3.6 | 1.4 |
| *Ancilla (Eburna)* Lamarck | Olividae | G | 64 | 119836 | 19 | 10 | X | 9.6 | 2.8 |
| *Scobinella* Conrad | Turridae | G | 63 | 119899 | 15 | 7 | X | 9.6 | 1.6 |
| *Tagelus (Mesopleura)* Conrad | Solecurtidae | B | 61 | 119960 | 3 | 2 | X | 2.6 | 1.6 |
| *Acila* H. & A. Adams | Nuculidae | B | 59 | 120019 | 7 | 3 | X | 8.6 | 6.9 |
| cypraeid* | Cypraeidae | G | 56 | 120075 | 12 | 6 | X | 11.6 | 1.4 |
| *Anadara* (s.l.)* | Arcidae | B | 55 | 120030 | 13 | 8 | X | 9.6 | 3.1 |
| *Cerithiopsis* Forbes & Hanley | Cerithiopsidae | G | 52 | 120182 | 15 | 10 | X | 9.6 | 1.4 |
| *Chlamys*[24] | Pectinidae | B | 51 | 120233 | 11 | 6 | X | 6.9 | 2.1 |
| *Fusiturricula* Woodring | Turridae | G | 51 | 120284 | 19 | 11 | X | 6.9 | 1.6 |
| *Terebra** Bruguière | Terebridae | G | 49 | 120333 | 13 | 10 | X | 8.6 | 1.7 |
| *Anachis* H. & A. Adams | Columbellidae | G | 48 | 120381 | 8 | 4 | X | 9.6 | 1.6 |
| *Arene** H. & A. Adams | Turbinidae | G | 46 | 120427 | 15 | 6 | X | 3.5 | 1.6 |
| *Xenophora* Fischer | Xenophoridae | G | 46 | 120473 | 19 | 9 | X | 4.3 | 2.8 |
| *Compsodrillia* ? Woodring | Turridae | G | 45 | 120518 | 12 | 6 | X | 6.9 | 1.6 |
| *Pitar* Romer | Veneridae | B | 44 | 120562 | 18 | 8 | X | 4.3 | 1.6 |
| *Dendostrea* ? Swainson | Ostreidae | B | 43 | 120605 | 15 | 9 | X | 8.6 | 1.7 |
| *Parvanachis* Radwin | Columbellidae | G | 43 | 120648 | 3 | 3 | X | 3.1 | 1.6 |
| corbulid* |  | B | 43 | 120691 | 6 | 5 | X | 8.6 | 2.6 |
| *Linga (Bellucina)* Dall | Lucinidae | B | 42 | 120733 | 14 | 10 | X | 11.6 | 3.1 |
| marginellid* |  | G | 41 | 120774 | 11 | 9 | X | 8.6 | 1.4 |
| *Tricolia* Risso | Turbinidae | G | 39 | 120813 | 4 | 3 | X | 8.6 | 2.6 |
| *Ficus* Röding | Ficidae | G | 38 | 120851 | 8 | 5 | X | 6.9 | 3.6 |
| *Heliacus*[25] d'Orbigny | Architectonicidae | G | 37 | 120888 | 20 | 14 | X | 9.6 | 1.6 |
| *Barleeia* Clark | Barleeidae | G | 37 | 120925 | 4 | 3 | X | 4.3 | 1.4 |
| *Agaronia* Gray | Olividae | G | 37 | 120962 | 18 | 10 | X | 11.6 | 1.6 |
| *Dendostrea* Swainson | Ostreidae | B | 36 | 120998 | 16 | 13 | X | 9.6 | 1.6 |
| *Angulus* Megerle | Tellinidae | B | 36 | 121034 | 8 | 5 | X | 11.6 | 1.7 |
| *Anadara (Cunearca)** ? Dall | Arcidae | B | 34 | 121068 | 6 | 6 | X | 4.3 | 1.6 |
| *Strombina (Strombina)* ? Mörch | Columbellidae | G | 33 | 121101 | 4 | 1 | X | 7.7 | 7.7 |
| *Noetia (Noetia)* Gray | Noetiidae | B | 32 | 121133 | 7 | 3 | X | 11.6 | 2.6 |
| *Tellina (Phyllodina)* Dall | Tellinidae | B | 31 | 121164 | 10 | 7 | X | 4.3 | 1.6 |
| *Eontia** MacNeil | Noetiidae | B | 30 | 121194 | 12 | 7 | X | 4.3 | 1.6 |
| *Eurytellina* ? Fischer | Tellinidae | B | 30 | 121224 | 5 | 4 | X | 11.6 | 1.6 |
| *Rhinoclavis (Ochetoclava)* Woodring | Cerithiidae | G | 28 | 121252 | 12 | 5 | X | 6.9 | 2.1 |
| *Balcis* Leach | Eulimidae | G | 27 | 121279 | 17 | 8 | X | 9.6 | 1.6 |
| *Subcancilla* ? Olsson & Harbison | Mitridae | G | 27 | 121306 | 1 | 1 | X | 1.4 | 1.4 |
| *Syntomodrillia* ? Woodring | Turridae | G | 27 | 121333 | 6 | 6 | X | 3.6 | 1.4 |
| *Cardiomya* A. Adams | Cuspidariidae | B | 26 | 121359 | 8 | 7 | X | 8.6 | 1.6 |

APPENDIX 2.—Continued.

| Genus and subgenus | Family | Class | Number of specimens | Cumulative number of specimens | Number of collections | Number of faunules | Used in ordinations | First occurrence (Ma) | Last occurrence (Ma) |
|---|---|---|---|---|---|---|---|---|---|
| *Miraclathurella* Woodring | Turridae | G | 24 | 121383 | 17 | 11 | X | 11.6 | 1.6 |
| *Granulina* ? Jousseaume | Marginellidae | G | 23 | 121406 | 1 | 1 | X | 3.6 | 3.6 |
| *Solariella* Wood | Trochidae | G | 23 | 121429 | 9 | 8 | X | 8.6 | 1.6 |
| *Linga* (*Pleurolucina*) Dall | Lucinidae | B | 23 | 121452 | 4 | 3 | X | 6.9 | 3.6 |
| *Natica* (*Natica*) ? Scopoli | Naticidae | G | 22 | 121474 | 10 | 7 | X | 9.6 | 2.8 |
| *Cassis* Scopoli | Cassidae | G | 21 | 121495 | 15 | 9 | X | 4.3 | 1.6 |
| *Bellaspira* Conrad | Turridae | G | 21 | 121516 | 6 | 5 | X | 7.7 | 1.6 |
| *Acar* Gray | Arcidae | B | 19 | 121535 | 11 | 7 | X | 3.6 | 1.4 |
| *Alvania* ? Risso | Rissoidae | G | 18 | 121553 | 1 | 1 | X | 1.4 | 1.4 |
| *Antillophos* (*Antillophos*) ? Woodring | Buccinidae | G | 18 | 121571 | 1 | 1 | X | 6.9 | 6.9 |
| *Ondina* de Folin | Pyramidellidae | G | 18 | 121589 | 6 | 6 | X | 4.3 | 1.4 |
| *Arene* (*Arene*) H. & A. Adams | Turbinidae | G | 16 | 121605 | 3 | 3 | X | 3.6 | 1.4 |
| neogastropod* |  | G | 14 | 121619 | 8 | 6 | X | 9.6 | 3.6 |
| *Spathochlamys* Waller | Pectinidae | B | 14 | 121633 | 6 | 5 | X | 3.5 | 1.6 |
| *Atrina* Gray | Pinnidae | B | 13 | 121646 | 4 | 4 | X | 11.6 | 6.9 |
| *Lunarca* ? Gray | Arcidae | B | 13 | 121659 | 2 | 1 | X | 3.6 | 3.6 |
| *Eulimastoma* ? Bartsch | Pyramidellidae | G | 13 | 121672 | 6 | 6 | X | 9.6 | 1.4 |
| *Bathygalea* (*Miogalea*) Woodring & Olsson | Cassidae | G | 13 | 121685 | 7 | 2 | X | 6.9 | 5.7 |
| *Euchelus* (*Mirachelus*) Woodring | Trochidae | G | 12 | 121697 | 4 | 4 | X | 3.6 | 1.4 |
| *Miraclathurella* ? Woodring | Turridae | G | 12 | 121709 | 4 | 3 | X | 3.6 | 2.1 |
| *Atys* Montfort | Haminoeidae | G | 12 | 121721 | 10 | 7 | X | 4.3 | 1.7 |
| *Agladrillia** ? | Turridae | G | 11 | 121732 | 8 | 6 | X | 11.6 | 1.6 |
| *Transennella* Dall | Veneridae | B | 11 | 121743 | 7 | 5 | X | 8.6 | 1.6 |
| *Olivella* (s.l.)* | Olividae | G | 11 | 121754 | 5 | 5 | X | 4.3 | 1.6 |
| *Antillophos* ? Woodring | Buccinidae | G | 10 | 121764 | 6 | 5 | X | 11.6 | 3.5 |
| *Lucina* (*Lepilucina*) Olsson | Lucinidae | B | 9 | 121773 | 2 | 1 | X | 4.3 | 4.3 |
| *Cosmioconcha* Dall | Columbellidae | G | 9 | 121782 | 7 | 6 | X | 8.6 | 1.6 |
| *Hindsia* A. Adams | Buccinidae | G | 9 | 121791 | 2 | 1 | X | 3.5 | 3.5 |
| *Thelecythara** Woodring | Turridae | G | 9 | 121800 | 3 | 2 | X | 3.5 | 1.6 |
| *Microgaza* ? Dall | Trochidae | G | 8 | 121808 | 2 | 2 | X | 7.7 | 3.6 |
| *Argopecten* ? Monterosato | Pectinidae | B | 8 | 121816 | 6 | 6 | X | 9.6 | 2.6 |
| *Calliostoma* ? Swainson | Trochidae | G | 7 | 121823 | 4 | 4 | X | 8.6 | 3.1 |
| *Phalium** Link | Cassidae | G | 7 | 121830 | 5 | 4 | X | 4.3 | 1.7 |
| *Cantharus** Röding | Buccinidae | G | 5 | 121835 | 3 | 2 | X | 8.6 | 1.6 |
| *Homalopoma* (*Leptothyropsis*) Woodring | Turbinidae | G | 4 | 121839 | 1 | 1 | X | 5.7 | 5.7 |
| *Chiodrillia* ? Woodring | Turridae | G | 4 | 121843 | 2 | 1 | X | 7.7 | 7.7 |
| *Merisca* Dall | Tellinidae | B | 3 | 121846 | 1 | 1 | X | 3.1 | 3.1 |
| *Vitrinella* ? C.B. Adams | Vitrinellidae | G | 2 | 121848 | 1 | 1 | X | 8.6 | 8.6 |
| *Irus* (*Irus*)* ? | Veneridae | B | 2 | 121850 | 1 | 1 | X | 8.6 | 8.6 |
| muricid* ? | Muricidae | G | 2 | 121852 | 2 | 2 | X | 8.6 | 8.6 |
| *Buridrillia* ? | Turridae | G | 2 | 121854 | 2 | 2 | X | 7.7 | 3.0 |
| *Hiatella* ? Daudin | Hiatellidae | B | 1 | 121855 | 1 | 1 | X | 8.6 | 8.6 |
| *Ringicula* (*Ringiculella*) ? Sacco | Ringiculidae | G | 1 | 121856 | 1 | 1 | X | 8.6 | 8.6 |
| *Careliopsis* ? Mörch | Pyramidellidae | G | 1 | 121857 | 1 | 1 | X | 3.0 | 3.0 |

APPENDIX 2.—Continued.

TAXONOMIC NOTES: Necessity has forced us to group some taxa for the analyses pending further study. This has been a consequence of: a) lack of a recently published systematic revision, b) difficulties in identification and consistent differentiation, c) simple lack of time, or more rarely, d) inadequate material. The tentative status of the groupings used (Monophyletic (M), Paraphyletic (P) or Unknown (U)), with respect to other taxa analyzed herein, is indicated in parentheses.

1. *Turritella*—all turritellids except *Vermicularia* Lamarck lumped here. In analysed collections a number of undescribed genus-level taxa occur. The few described taxa include: *Bactrospira* Cossmann, *Broderiptella* Olsson, *Torcula* Gray. (U).

2. *Nassarius*—considered *sensu latus*; includes taxa assignable to the "subgenera" *Hinia* Gray, *Nanarius* Woodring and *Uzita* H. and A. Adams. (M).

3. *Conus*—includes a number of unresolved "cone" taxa traditionally treated as subgenera of *Conus* Linnaeus. (M).

4. *Cadulus*—includes the following identified taxa belonging to the Gadilidae: *Cadulus* Philippi, *Gadila* Gray, *Polyschides* Pilsbry and Sharp and possibly some specimens assignable to *Gadilopsis* Woodring, which has otherwise been treated separately as has *Siphonodentalium* Sars. (U).

5. *Anadara* (*Cunearca*)—included are species that may fall within the original concept of *Esmerarca* Olsson. (U).

6. *Cancellaria* (s.l.)—in addition to the nominotypical subgenus, the following taxa, often considered to be subgenera of *Cancellaria* Lamarck, are included here: *Bivetiella* Wenz, *Charcolleria* Olsson, *Euclia* H. and A. Adams, *Hertleinia* Marks, *Massyla* H. and A. Adams and *Pyruclia* Olsson. (M?).

7. *Lirophora*—includes both *Lirophora* Conrad and *Panchione* Olsson. The other 'chionine' genera analyzed (*Chione*, *Chionopsis*) have been treated separately. (M, according to Roopnarine, 1996).

8. Caecid—includes all decollate caecids with regularly expanding shell diameters, with one exception, *Micranellum* Bartsch, which was analyzed separately. Apart from this, the grouping corresponds with the traditional usage of the genus *Caecum* Fleming (s.l.). Includes *Caecum* (s.s.), *Elephantanellum* Bartsch, *Elephantulum* Carpenter and *Brochina* Gray. *Meioceras* Carpenter had been treated separately. (Pa according to Bandel, 1996).

9. *Dentalium* (s.l.)—the following genera of the Dentaliidae have been lumped here: *Dentalium* Linnaeus, *Antalis* H. and A. Adams, *Paradentalium* Cotton and Godfrey. The dentalnd genera *Fissidentalium* Fischer and *Tesseracme* Pilsbry and Shar have been treated separately. (U).

10. *Trigoniocardia* (s.l.)—includes subgenera *Trigoniocardia* Dall and *Apiocardia* Olsson. (M).

11. *Strombus*—includes subgenera *Strombus* Linnaeus, *Lentigo* Jousseaume, *Tricornis* Jousseaume and specimens referred to "cf. *Tricornis*". (M).

12. Turbonilline—included here are a range of turreted, axially sculptured pyramidellids with a straight columella typically lacking, or with a very slight, columellar fold. These taxa, sometimes grouped as the subfamily Turbonillinae, are often conservatively considered to be subgenera of, or even synonymous with, *Turbonilla* Risso. Includes: *Turbonilla*, *Chemnitzia* d'Orbigny, *Dunkeria* Carpenter, *Pyrgiscilla* ? Laws, *Pyrgiscus* Philippi, *Pyrgolampros* Sacco and *Strioturbonilla* Sacco. Treated separately: *Bartschella* Iredale, *Mormula* A. Adams, *Ptycheulimella* Sacco, *Ugartea* Bartsch. (U).

13. *Mitra*—includes subgenera *Mitra* (s.s.) Lamarck and *Nebularia* Swainson. (U).

14. Rissoine—corresponds to the subfamily Rissoinae. Presently lumped here are the following: *Rissoina* (*R.*) d'Orbigny, *Rissoina* (*Phosinella*) Mörch, *Folinia* Crosse, *Schwartziella* (*Pandalosia*) Laseron and *Zebina* (*Z.*) H. and A. Adams. (M; Ponder, 1985).

15. Pyramidelline—we have grouped here some taxa typically considered to be subgenera of *Pyramidella* Lamarck. Includes the nominal taxa: *Callolongchaeus* Dall and Bartsch, *Longchaeus* Mörch and *Pharcidella* Dall. (M?).

16. Eulimid—the family Eulimidae is a systematically diverse but notoriously difficult group to identify by shell characters alone. We have simply grouped all eulimids together with the exclusion of the easily identifiable taxa *Balcis* Leach and *Niso* Risso. (P?).

17. *Clathrodrillia*—lumped under this name are specimens assignable to the genera *Clathrodrillia* Dall and *Fenimorea* Bartsch. (U).

18. *Teinostoma*—includes *Teinostoma* H. and A. Adams (s.l.) as well as taxa placed in the nominal subgenera *Aepystoma* Woodring, *Idioraphe* Pilsbry and *Pseudorotella* Fischer. (U).

19. Typhine—corresponds to the traditional subfamily Typhinae. Includes *Typhis* (*Talityphis*) Jousseaume, *T.* (*Typhinellus*) Jousseaume, *Siphonochelus* (*S.*) Jousseaume, *S.* (*Laevityphis*) Cossmann and *S.* (*Pilsbrytyphis*) Woodring. (M?).

20. Carditesine—includes the genera *Glyptoactis* (*G.*) Stewart and *Cardites* Link. (M).

21. Triphorid—the majority of specimens belonging to the subfamily Triphorinae lack their protoconch and consequently are unidentifiable to generic level. Identifiable genera grouped here include *Isotriphora* Cotton and Godfrey and *Tetraphora* Laseron. The dextral genus *Metaxia* Monterosato (Metaxiinae) has been analyzed separately. (M?).

22. *Solariorbis*—includes *Solariorbis* (*S.*) Conrad and taxa referred to *Solariorbis* (s.l.). The subgenus *Hapalorbis* Woodring has been analyzed separately. (U).

23. *Latirus*—includes subgenera *Latirus* Montfort and *Polygona* Schumacher. (M).

24. *Chlamys*—includes specimens possibly assignable to *Spathochlamys* Waller, which is otherwise treated separately. (U).

25. *Heliacus* (s.l.)—includes subgenera *Heliacus* d'Orbigny and *Torinista* Iredale. (M).

## APPENDIX 3

### MOST ABUNDANT TAXA

Listed are the 25 most abundant taxa per faunule, based on numbers of specimens obtained from each of the 37 faunules listed in Table 2.

| Genus and subgenus | Class | Number of Specimens |
|---|---|---|
| 1. Swan Cay (Bocas del Toro Basin). PPP: 1995. | | |
| *Olivella* (*Minioliva*) | G | 367 |
| *Limopsis* | B | 110 |
| *Nassarius* (s.l.) | G | 87 |
| *Granula* | G | 71 |
| *Granulina* | G | 64 |
| *Antillophos* (*Antillophos*) | G | 41 |
| *Saccella* | B | 32 |
| *Volvarina* | G | 32 |
| rissoine | G | 31 |
| *Subcancilla* ? | G | 27 |
| *Crassinella* | B | 22 |
| *Alvania* | G | 21 |
| *Barleeia* | G | 21 |
| *Syntomodrillia* ? | G | 20 |
| *Conus* | G | 19 |
| *Alvania* ? | G | 18 |
| *Teinostoma* | G | 18 |
| *Olivella* (*Macgintiella*) | G | 15 |
| *Polystira* | G | 15 |
| *Hyotissa* | B | 15 |
| turbonilline | G | 13 |
| *Metula* | G | 13 |
| *Arene* (*Arene*) | G | 13 |
| *Arcopsis* | B | 12 |
| *Cerithiopsis* | G | 12 |
| 2. Cemetery Pueblo Nuevo (Limon Basin). PPP: 631. | | |
| *Caryocorbula* | B | 125 |
| *Argopecten* | B | 51 |
| *Gouldia* | B | 45 |
| *Anadara* (*Rasia*) | B | 29 |
| *Limopsis* | B | 17 |
| *Petaloconchus* | G | 14 |
| *Crassinella* | B | 13 |
| *Varicorbula* | B | 11 |
| *Solariorbis* | G | 10 |
| *Diodora* | G | 7 |
| *Nassarius* (s.l.) | G | 6 |
| *Cyclopecten* | B | 6 |
| *Acar* | B | 6 |
| *Cerithiopsis* | G | 6 |
| *Arene* | G | 6 |
| *Jupiteria* | B | 6 |
| *Nucula* (*Lamellinucula*) | B | 5 |
| *Chama* | B | 5 |
| *Saccella* | B | 4 |
| *Sulcoretusa* | G | 4 |
| *Heliacus* | G | 4 |
| triphorid | G | 3 |
| *Leionucula* | B | 3 |
| caecid | G | 3 |
| *Parvilucina* (s.l.) | B | 3 |
| *Tucetona* | B | 3 |
| *Volvarina* | G | 3 |
| 3. Upper Lomas del Mar East (reef) (Limon Basin). PPP: 468,469, 628, 942, 943, 944, 948, 949, 950, 951, 962, 963. | | |
| *Turritella* | G | 1194 |
| *Conus* | G | 397 |
| *Mitra* | G | 291 |
| *Antillophos* (*Antillophos*) | G | 233 |
| *Argopecten* | B | 214 |
| *Dimya* | B | 212 |
| *Voluta* | G | 207 |
| *Volvarina* | G | 187 |
| *Siliquaria* | G | 171 |
| *Volvarina* ? | G | 152 |
| *Olivella* (*Macgintiella*) | G | 131 |
| *Haustellum* | G | 123 |
| *Olivella* (*Minioliva*) | G | 106 |
| *Polystira* | G | 97 |
| *Saccella* | B | 93 |
| *Knefastia* | G | 93 |
| *Diodora* | G | 80 |
| *Barbatia* (*Barbatia*) | B | 75 |
| *Nassarius* (s.l.) | G | 74 |
| *Latirus* | G | 70 |
| *Dentalium* (s.l.) | S | 66 |
| *Lucinoma* ? | B | 65 |
| *Hindsiclava* | G | 62 |
| *Coralliophila* | G | 55 |
| *Flabellipecten* | B | 51 |
| 4. Empalme (Limon Basin). PPP: 715, 718, 719, 759, 1987. | | |
| *Argopecten* | B | 310 |
| *Luria* | G | 286 |
| *Caryocorbula* | B | 248 |
| *Bulla* | G | 168 |
| *Macrocypraea* | G | 85 |
| *Crassostrea* | B | 81 |
| *Strombus* | G | 76 |
| *Zonaria* | G | 47 |
| *Parvanachis* | G | 41 |
| *Conus* | G | 36 |
| cypraeid | G | 32 |
| turbonilline | G | 31 |
| *Nassarius* (s.l.) | G | 27 |
| *Macrocallista* (*Megapitaria*) | B | 26 |
| *Trigoniocardia* (s.l.) | B | 25 |
| *Lirophora* | B | 23 |
| *Plicatula* | B | 22 |
| triphorid | G | 21 |
| *Cadulus* | S | 21 |
| *Axinactis* (*Glycymerella*) | B | 20 |
| *Oliva* (*Oliva*) | G | 20 |
| *Anadara* (*Cunearca*) ? | B | 17 |
| *Pitar* | B | 17 |
| *Barbatia* (*Barbatia*) | B | 16 |
| *Saccella* | B | 16 |
| 5. Cangrejos Creek (Limon Basin). PPP: 648, 649, 651, 653, 657. | | |
| *Dosinia* | B | 80 |
| *Dentalium* (s.l.) | S | 64 |
| *Cadulus* | S | 56 |
| rissoine | G | 45 |

APPENDIX 3.—Continued.

| Genus and subgenus | Class | Number of Specimens |
|---|---|---|
| *Olivella (Macgintiella)* | G | 42 |
| *Olivella (Minioliva)* | G | 37 |
| *Nassarius* (s.l.) | G | 35 |
| *Alvania* | G | 34 |
| *Kurtziella (Kurtziella)* | G | 28 |
| *Styliola* | G | 27 |
| *Limopsis* | B | 21 |
| *Anachis* | G | 19 |
| *Jupiteria* | B | 13 |
| *Glyphostoma (Glyphostoma)* | G | 12 |
| turbonilline | G | 12 |
| *Kurtziella (Cryoturris)* | G | 12 |
| *Teinostoma* | G | 11 |
| *Carinodrillia* | G | 11 |
| *Saccella* | B | 10 |
| *Stigmaulax* | G | 10 |
| *Trigonulina* | B | 10 |
| *Diacria* | G | 9 |
| *Ringicula (Ringiculella)* | G | 9 |
| turrid | G | 9 |
| *Polinices* | G | 7 |
| *Euchelus (Mirachelus)* | G | 7 |
| *Thelecythara* | G | 7 |

6. Lower Lomas del Mar East (non reef) (Limon Basin). PPP: 464, 465, 466, 467, 634, 635, 710, 757, 1982, 1988.

| | | |
|---|---|---|
| *Caryocorbula* | B | 853 |
| *Siliquaria* | G | 519 |
| *Turritella* | G | 292 |
| *Conus* | G | 285 |
| *Volvarina* | G | 255 |
| *Olivella (Minioliva)* | G | 206 |
| *Nassarius* (s.l.) | G | 176 |
| *Argopecten* | B | 174 |
| scaphopod | S | 145 |
| *Dentalium* (s.l.) | S | 131 |
| *Vermicularia* | G | 116 |
| *Crassinella* | B | 116 |
| triphorid | G | 96 |
| *Voluta* | G | 91 |
| *Gouldia* | B | 88 |
| *Dimya* | B | 88 |
| *Antillophos (Antillophos)* | G | 82 |
| *Cadulus* | S | 78 |
| turrid | G | 71 |
| turbonilline | G | 69 |
| *Alabina* | G | 62 |
| *Granulina* | G | 58 |
| *Myrtea* | B | 54 |
| *Polystira* | G | 54 |
| *Diodora* | G | 53 |

7. Northwest Escudo de Veraguas (Bocas del Toro Basin). PPP: 176, 177, 178, 1974.

| | | |
|---|---|---|
| *Olivella (Minioliva)* | G | 97 |
| *Saccella* | B | 51 |
| *Antillophos (Antillophos)* | G | 36 |
| *Oliva (Oliva)* | G | 34 |
| *Olivella (Macgintiella)* | G | 27 |
| *Cadulus* | S | 20 |
| *Anadara (Rasia)* | B | 16 |
| *Haustellum* | G | 14 |
| *Argopecten* | B | 13 |
| *Agladrillia (Agladrillia)* | G | 12 |
| *Crassispira (Crassispira)* | G | 11 |
| *Tucetona* | B | 10 |
| *Conus* | G | 10 |
| *Volvarina* | G | 9 |
| *Leionucula* | B | 8 |
| *Dentalium* (s.l.) | S | 6 |
| *Miraclathurella* ? | G | 5 |
| *Natica (Naticarius)* | G | 5 |
| *Metula* | G | 4 |
| *Serpulorbis* | G | 3 |
| *Sincola (Sinaxila)* | G | 3 |
| *Strombus* | G | 3 |
| *Cosmioconcha* | G | 3 |
| *Polystira* | G | 2 |
| *Chlamys* | B | 2 |
| *Miraclathurella* | G | 2 |
| *Jupiteria* | B | 2 |
| eulimid | G | 2 |
| *Subcancilla* | G | 2 |
| *Olivella* (s.l.) | G | 2 |

8. Fish Hole (Bocas del Toro Basin). PPP: 1254, 1256, 1304.

| | | |
|---|---|---|
| *Olivella (Minioliva)* | G | 30 |
| *Conus* | G | 21 |
| *Anadara (Rasia)* | B | 16 |
| *Voluta* | G | 15 |
| *Tucetona* | B | 12 |
| *Saccella* | B | 8 |
| carditesine | B | 7 |
| *Nassarius* (s.l.) | G | 7 |
| *Polystira* | G | 6 |
| *Dentimargo* | G | 6 |
| *Syntomodrillia* | G | 6 |
| *Knefastia* | G | 6 |
| *Volvarina* | G | 6 |
| *Antillophos (Antillophos)* | G | 5 |
| *Sconsia* | G | 5 |
| *Granulina* | G | 5 |
| *Oliva (Oliva)* | G | 5 |
| *Axinactis (Glycymerella)* | B | 4 |
| *Rhinoclavis (Ochetoclava)* | G | 4 |
| *Solenosteira* | G | 4 |
| *Cassis* | G | 4 |
| rissoine | G | 4 |
| triphorid | G | 4 |
| *Crassinella* | B | 4 |
| *Acar* | B | 4 |

9. Ground Creek (Bocas del Toro Basin). PPP: 1285, 1286.

| | | |
|---|---|---|
| *Chione* | B | 450 |
| *Nucula (Nucula)* | B | 155 |
| *Bulla* | G | 117 |
| *Saccella* | B | 74 |
| *Lucinisca* | B | 66 |
| *Tagelus (Mesopleura)* | B | 60 |
| *Macrocallista (Megapitaria)* | B | 59 |

APPENDIX 3.—Continued.

| Genus and subgenus | Class | Number of Specimens |
|---|---|---|
| *Eurytellina* | B | 51 |
| caecid | G | 50 |
| *Varicorbula* | B | 42 |
| *Argopecten* | B | 42 |
| *Parvilucina* (s.l.) | B | 42 |
| *Meioceras* | G | 36 |
| *Alabina* | G | 29 |
| *Stigmaulax* | G | 24 |
| *Dosinia* | B | 24 |
| *Noetia* (*Noetia*) | B | 23 |
| *Angulus* | B | 21 |
| *Tricolia* | G | 19 |
| *Laevicardium* | B | 19 |
| *Anadara* (*Cunearca*) | B | 19 |
| *Volvulella* (*Volvulella*) | G | 18 |
| *Strombus* | G | 17 |
| turbonilline | G | 15 |
| *Acteocina* | G | 14 |
| *Conus* | G | 14 |

10. North Central Escudo de Veraguas (Bocas del Toro Basin). PPP: 179, 180, 358, 359, 361, 362, 363, 364.

| Genus and subgenus | Class | Number of Specimens |
|---|---|---|
| *Olivella* (*Macgintiella*) | G | 443 |
| *Nassarius* (s.l.) | G | 366 |
| *Gadilopsis* | S | 195 |
| *Antillophos* (*Antillophos*) | G | 171 |
| *Dentimargo* | G | 160 |
| *Volvarina* | G | 147 |
| *Kelliella* | B | 145 |
| *Saccella* | B | 131 |
| *Cavolinia* | G | 125 |
| *Sulcoretusa* | G | 111 |
| rissoine | G | 110 |
| *Cadulus* | S | 95 |
| *Crassinella* | B | 89 |
| *Sincola* (*Sinaxila*) ? | G | 87 |
| *Pectunculina* | B | 86 |
| *Styliola* | G | 84 |
| *Strioterebrum* | G | 78 |
| *Caryocorbula* | B | 74 |
| *Acteocina* | G | 65 |
| *Alabina* | G | 63 |
| *Gouldia* | B | 61 |
| *Turritella* | G | 61 |
| *Yoldia* | B | 57 |
| *Abra* | B | 56 |
| *Eulimella* (*Ebalina*) | G | 56 |

11. Rio Limoncito (Limon Basin). PPP: 463.

| Genus and subgenus | Class | Number of Specimens |
|---|---|---|
| *Tucetona* | B | 55 |
| *Turritella* | G | 9 |
| scaphopod | S | 9 |
| *Parvilucina* (s.l.) | B | 6 |
| caecid | G | 5 |
| *Limacina* | G | 4 |
| *Anadara* (*Rasia*) | B | 4 |
| *Crassinella* | B | 4 |
| *Ringicula* (*Ringiculella*) | G | 4 |
| *Strombus* | G | 4 |
| *Nucula* (*Lamellinucula*) | B | 3 |
| *Polystira* | G | 3 |
| *Cyclopecten* | B | 3 |
| *Trachycardium* (s.l.) | B | 2 |
| *Conus* | G | 2 |
| *Nucula* (*Nucula*) | B | 2 |
| *Oliva* (*Oliva*) | G | 2 |
| *Architectonica* | G | 2 |
| *Sulcoretusa* | G | 2 |
| *Saccella* | B | 2 |
| *Dentalium* (s.l.) | S | 2 |
| *Hindsiclava* | G | 2 |
| *Cadulus* | S | 1 |
| *Noetia* | B | 1 |
| *Buridrillia* ? | G | 1 |
| *Stigmaulax* | G | 1 |
| *Acteocina* | G | 1 |
| *Agaronia* | G | 1 |
| *Knefastia* | G | 1 |
| *Voluta* | G | 1 |
| *Rhinoclavis* (*Ochetoclava*) | G | 1 |
| *Careliopsis* ? | G | 1 |
| *Atys* | G | 1 |
| *Meioceras* | G | 1 |
| *Anadara* (*Cunearca*) ? | B | 1 |
| *Petaloconchus* | G | 1 |

12. Chocolate Buenos Aires (Limon Basin). PPP: 1083, 1772, 1773.

| Genus and subgenus | Class | Number of Specimens |
|---|---|---|
| *Caryocorbula* | B | 286 |
| *Nucula* (*Nucula*) | B | 254 |
| *Chionopsis* | B | 111 |
| *Alabina* | G | 56 |
| *Cadulus* | S | 46 |
| *Acteocina* | G | 33 |
| scaphopod | S | 29 |
| *Ostreola* | B | 27 |
| *Ringicula* (*Ringiculella*) | G | 20 |
| *Vermicularia* | G | 10 |
| *Anadara* (*Rasia*) | B | 10 |
| *Cardiomya* | B | 9 |
| *Saccella* | B | 9 |
| *Olivella* (*Olivella*) | G | 9 |
| *Dentalium* (s.l.) | S | 9 |
| *Pitar* | B | 8 |
| *Bulla* | G | 8 |
| *Eurytellina* | B | 7 |
| *Olivella* (*Minioliva*) | G | 7 |
| *Macrocallista* (*Megapitaria*) | B | 5 |
| *Eulimastoma* | G | 4 |
| *Ithycythara* | G | 4 |
| *Dendostrea* | B | 4 |
| *Anadara* (s.l.) | B | 4 |
| *Epitonium* (*Asperiscala*) | G | 3 |
| *Teinostoma* | G | 3 |
| *Cylichnella* | G | 3 |
| eulimid | G | 3 |
| pyramidelline | G | 3 |
| triphorid | G | 3 |
| *Nassarius* (s.l.) | G | 3 |
| *Merisca* | B | 3 |
| *Ondina* | G | 3 |

APPENDIX 3.—Continued.

| Genus and subgenus | Class | Number of Specimens |
|---|---|---|
| 13. Bomba (Limon Basin). PPP: 451, 452, 455, 456, 457, 458, 459, 460, 461, 462, 668, 669, 672, 678, 686, 691, 758, 1726, 1727, 1728, 1729, 1730, 1731, 1732, 1733, 1764, 1983, 1984, 1986. NMB: 13836, 17477, 17478, 17479, 17480. | | |
| *Crassinella* | B | 3327 |
| *Olivella* (*Dactylidella*) | G | 1238 |
| *Anadara* (*Cunearca*) | B | 994 |
| *Caryocorbula* | B | 687 |
| *Turritella* | G | 610 |
| *Olivella* (*Olivella*) | G | 550 |
| *Strioterebrum* | G | 481 |
| *Parvilucina* (s.l.) | B | 469 |
| *Tucetona* | B | 453 |
| *Alabina* | G | 449 |
| caecid | G | 401 |
| *Prunum* | G | 361 |
| *Acteocina* | G | 349 |
| *Persicula* | G | 340 |
| *Stigmaulax* | G | 324 |
| *Natica* (*Naticarius*) | G | 276 |
| *Varicorbula* | B | 273 |
| *Nassarius* (s.l.) | G | 269 |
| *Sincola* (*Sincola*) | G | 231 |
| *Strombus* | G | 221 |
| *Dentalium* (s.l.) | S | 220 |
| *Macrocallista* (*Megapitaria*) | B | 212 |
| *Conus* | G | 182 |
| *Limacina* | G | 175 |
| *Voluta* | G | 154 |
| 14. Agua (Limon Basin). PPP: 696, 697. | | |
| *Olivella* (*Dactylidella*) | G | 262 |
| *Persicula* | G | 169 |
| *Tucetona* | B | 57 |
| *Conus* | G | 53 |
| *Laevidentalium* | S | 37 |
| *Stigmaulax* | G | 30 |
| pyramidelline | G | 29 |
| *Prunum* | G | 28 |
| *Strioterebrum* | G | 27 |
| caecid | G | 21 |
| *Acteocina* | G | 12 |
| *Sincola* (*Sincola*) | G | 11 |
| *Niso* | G | 11 |
| *Turritella* | G | 9 |
| *Sincola* (*Sinaxila*) | G | 8 |
| *Mitra* | G | 8 |
| *Strombus* | G | 7 |
| *Parvilucina* (s.l.) | B | 7 |
| *Terebra* | G | 5 |
| *Lirophora* | B | 3 |
| *Nassarius* (s.l.) | G | 3 |
| turrid | G | 3 |
| *Polinices* | G | 3 |
| *Anadara* (*Cunearca*) ? | B | 2 |
| *Oliva* (*Oliva*) | G | 2 |
| *Voluta* | G | 2 |
| *Cancellaria* (s.l.) | G | 2 |
| *Eontia* | B | 2 |

| Genus and subgenus | Class | Number of Specimens |
|---|---|---|
| 15. Bruno Bluff (Bocas del Toro Basin). PPP: 376, 379, 381, 1975. | | |
| *Varicorbula* | B | 225 |
| *Caryocorbula* | B | 90 |
| *Anadara* (*Rasia*) | B | 77 |
| *Parvilucina* (s.l.) | B | 72 |
| *Gouldia* | B | 45 |
| *Olivella* (*Niteoliva*) | G | 40 |
| *Alabina* | G | 39 |
| *Saccella* | B | 36 |
| naticid | G | 27 |
| *Moerella* | B | 22 |
| pyramidelline | G | 21 |
| *Turritella* | G | 21 |
| *Gadilopsis* | S | 19 |
| *Linga* (*Bellucina*) | B | 19 |
| *Trigoniocardia* (s.l.) | B | 17 |
| *Crassinella* | B | 16 |
| *Agladrillia* (*Agladrillia*) | G | 16 |
| *Calyptraea* | G | 16 |
| *Tucetona* | B | 16 |
| *Acteocina* | G | 15 |
| *Polystira* | G | 15 |
| *Meioceras* | G | 14 |
| *Bathoxiphus* | S | 13 |
| *Dimya* | B | 13 |
| *Argopecten* | B | 13 |
| 16. Cayo Agua: West side Punta Norte (Bocas del Toro Basin). PPP: 195, 196, 197, 198, 470, 471, 472, 473. | | |
| *Varicorbula* | B | 436 |
| *Tucetona* | B | 379 |
| *Caryocorbula* | B | 343 |
| *Argopecten* | B | 145 |
| *Cadulus* | S | 109 |
| *Alabina* | G | 104 |
| *Turritella* | G | 103 |
| *Cyclopecten* | B | 87 |
| *Petaloconchus* | G | 83 |
| *Crassinella* | B | 71 |
| turbonilline | G | 51 |
| *Plicatula* | B | 49 |
| *Trigoniocardia* (s.l.) | B | 45 |
| *Saccella* | B | 40 |
| *Cavolinia* | G | 40 |
| *Acteocina* | G | 35 |
| *Anadara* (*Rasia*) | B | 32 |
| *Chama* | B | 32 |
| *Volvarina* | G | 23 |
| caecid | G | 19 |
| scaphopod | S | 17 |
| *Crenella* | B | 16 |
| *Flabellipecten* | B | 16 |
| *Xenophora* | G | 15 |
| *Sulcoretusa* | G | 14 |
| 17. Quitaria (Limon Basin). PPP: 449, 450, 679, 695, 1734, 1735, 1985. | | |
| *Olivella* (*Dactylidella*) | G | 2295 |
| *Turritella* | G | 950 |
| *Olivella* (*Olivella*) | G | 885 |

APPENDIX 3.—Continued.

| Genus and subgenus | Class | Number of Specimens |
|---|---|---|
| *Crassinella* | B | 840 |
| *Sincola (Sincola)* | G | 702 |
| *Nassarius* (s.l.) | G | 602 |
| *Alabina* | G | 602 |
| *Anadara (Cunearca)* | B | 575 |
| *Caryocorbula* | B | 486 |
| caecid | G | 455 |
| *Tucetona* | B | 243 |
| *Macrocallista (Megapitaria)* | B | 208 |
| *Stigmaulax* | G | 207 |
| *Persicula* | G | 176 |
| *Anadara (Potiarca)* | B | 158 |
| *Parvilucina* (s.l.) | B | 146 |
| *Ringicula (Ringiculella)* | G | 143 |
| *Strioterebrum* | G | 143 |
| *Agladrillia (Agladrillia)* | G | 143 |
| *Strombus* | G | 135 |
| *Volvarina* | G | 119 |
| *Cylichnella* | G | 111 |
| turrid | G | 110 |
| *Prunum* | G | 105 |
| *Acteocina* | G | 99 |

18. Rio Vizcaya (Limon Basin). PPP: 925, 931, 932, 933, 935, 937, 1082.

| Genus and subgenus | Class | Number of Specimens |
|---|---|---|
| *Olivella (Dactylidella)* | G | 439 |
| *Anadara (Potiarca)* | B | 114 |
| *Prunum* | G | 68 |
| *Natica (Naticarius)* | G | 48 |
| *Anadara (Rasia)* | B | 41 |
| *Turritella* | G | 36 |
| *Conus* | G | 23 |
| *Axinactis (Glycymerella)* | B | 18 |
| *Stigmaulax* | G | 17 |
| *Strioterebrum* | G | 15 |
| *Anadara (Cunearca)* | B | 15 |
| *Noetia* | B | 13 |
| *Sincola (Sinaxila)* | G | 12 |
| *Volvarina* | G | 12 |
| *Dosinia* | B | 11 |
| *Caryocorbula* | B | 10 |
| *Hindsia* | G | 9 |
| *Strombus* | G | 8 |
| *Voluta* | G | 8 |
| *Chionopsis* | B | 8 |
| *Polinices* | G | 5 |
| *Cancellaria* (s.l.) | G | 4 |
| *Oliva (Oliva)* | G | 4 |
| *Eurytellina* | B | 3 |
| *Volvarina* ? | G | 3 |
| *Tucetona* | B | 3 |
| *Strombinophos* | G | 3 |
| *Antillophos (Antillophos)* | G | 3 |

19. Santa Rita (Limon Basin). PPP: 709, 723.

| Genus and subgenus | Class | Number of Specimens |
|---|---|---|
| *Tucetona* | B | 176 |
| *Cyclopecten* | B | 72 |
| *Eucrassatella (Eucrassatella)* | B | 32 |
| *Myrtea* | B | 14 |
| *Varicorbula* | B | 11 |
| *Volvarina* | G | 9 |
| *Conus* | G | 9 |
| *Sconsia* | G | 8 |
| *Arcopsis* | B | 6 |
| carditesine | B | 6 |
| *Crassinella* | B | 6 |
| *Anadara (Rasia)* | B | 6 |
| *Flabellipecten* | B | 5 |
| *Trachycardium* (s.l.) | B | 5 |
| *Gouldia* | B | 5 |
| *Laevidentalium* | S | 5 |
| *Arene* | G | 5 |
| *Crucibulum (Crucibulum)* | G | 5 |
| *Anomia* | B | 5 |
| *Barbatia (Barbatia)* | B | 4 |
| *Plicatula* | B | 4 |
| *Dentalium* (s.l.) | S | 4 |
| *Spathochlamys* | B | 4 |
| *Strombus* | G | 3 |
| *Architectonica* | G | 3 |
| *Voluta* | G | 3 |
| triphorid | G | 3 |
| *Marginella* | G | 3 |
| *Nassarius* (s.l.) | G | 3 |
| *Nucula (Lamellinucula)* | B | 3 |
| *Phalium* | G | 3 |

20. Northeast Escudo de Veraguas (Bocas del Toro Basin). PPP: 365, 366, 367, 368.

| Genus and subgenus | Class | Number of Specimens |
|---|---|---|
| *Olivella (Niteoliva)* | G | 136 |
| *Nassarius* (s.l.) | G | 127 |
| *Crassinella* | B | 105 |
| *Volvarina* | G | 94 |
| *Anadara (Rasia)* | B | 88 |
| *Caryocorbula* | B | 82 |
| *Saccella* | B | 74 |
| *Kelliella* | B | 71 |
| rissoine | G | 71 |
| *Cavolinia* | G | 64 |
| *Gadilopsis* | S | 59 |
| *Dentimargo* | G | 58 |
| *Sulcoretusa* | G | 53 |
| *Tellina (Scissula)* | B | 50 |
| *Gouldia* | B | 49 |
| *Antillophos (Antillophos)* | G | 47 |
| *Polinices* | G | 44 |
| *Alabina* | G | 42 |
| *Argopecten* | B | 42 |
| *Strioterebrum* | G | 41 |
| *Marginella* ? | G | 38 |
| *Parvilucina* (s.l.) | B | 37 |
| *Abra* | B | 36 |
| *Pectunculina* | B | 34 |
| *Styliola* | G | 33 |

21. Southeast Escudo de Veraguas (Bocas del Toro Basin). PPP: 168, 170, 431, 478, 479, 480, 481, 482, 483.

| Genus and subgenus | Class | Number of Specimens |
|---|---|---|
| *Antillophos (Antillophos)* | G | 199 |
| *Gadilopsis* | S | 149 |
| *Cadulus* | S | 132 |

APPENDIX 3.—Continued.

| Genus and subgenus | Class | Number of Specimens |
|---|---|---|
| *Saccella* | B | 131 |
| *Nassarius* (s.l.) | G | 98 |
| *Eulimella* (*Ebalina*) | G | 73 |
| *Dentalium* (s.l.) | S | 69 |
| *Volvarina* | G | 65 |
| *Conus* | G | 64 |
| *Bathoxiphus* | S | 64 |
| *Olivella* (*Minioliva*) | G | 60 |
| rissoine | G | 51 |
| *Strioterebrum* | G | 48 |
| *Leionucula* | B | 45 |
| *Anadara* (*Rasia*) | B | 40 |
| *Dentimargo* | G | 40 |
| *Microgaza* | G | 37 |
| *Parvilucina* (s.l.) | B | 33 |
| *Architectonica* | G | 32 |
| *Olivella* (*Macgintiella*) | G | 31 |
| turbonilline | G | 27 |
| *Styliola* | G | 26 |
| *Haustellum* | G | 24 |
| *Granulina* ? | G | 23 |
| *Volvulella* (*Volvulella*) | G | 22 |
| *Compsodrillia* ? | G | 22 |

22. Cayo Agua: Pt Tiburon (Bocas del Toro Basin). PPP: 294, 295, 296, 297, 335, 337, 339, 340, 341.

| Genus and subgenus | Class | Number of Specimens |
|---|---|---|
| *Olivella* (*Dactylidella*) | G | 559 |
| *Caryocorbula* | B | 420 |
| *Tucetona* | B | 262 |
| *Turritella* | G | 160 |
| *Crassinella* | B | 155 |
| *Argopecten* | B | 117 |
| *Acteocina* | G | 86 |
| *Oliva* (*Oliva*) | G | 82 |
| *Anadara* (*Rasia*) | B | 75 |
| *Varicorbula* | B | 74 |
| *Gouldia* | B | 69 |
| *Cadulus* | S | 66 |
| *Parvilucina* (s.l.) | B | 57 |
| *Persicula* | G | 57 |
| *Alabina* | G | 53 |
| *Strombus* | G | 53 |
| *Nucula* (*Lamellinucula*) | B | 47 |
| *Olivella* (*Macgintiella*) | G | 43 |
| *Volvarina* | G | 42 |
| *Ringicula* (*Ringiculella*) | G | 41 |
| *Strioterebrum* | G | 40 |
| *Natica* (*Natica*) | G | 39 |
| turbonilline | G | 38 |
| *Stigmaulax* | G | 36 |
| *Ervilia* | B | 34 |

23. Cayo Agua: Pt Nispero West (Bocas del Toro Basin). PPP: 318, 323, 325, 326, 330, 1303.

| Genus and subgenus | Class | Number of Specimens |
|---|---|---|
| *Turritella* | G | 471 |
| *Plicatula* | B | 65 |
| *Tucetona* | B | 65 |
| *Oliva* (*Oliva*) | G | 53 |
| *Caryocorbula* | B | 52 |
| *Varicorbula* | B | 33 |
| *Saccella* | B | 26 |
| *Axinactis* (*Glycymerella*) | B | 25 |
| *Tellina* (*Phyllodina*) | B | 23 |
| *scaphopod* | S | 23 |
| *Strombus* | G | 20 |
| *Nucula* (*Nucula*) | B | 19 |
| *Prunum* | G | 17 |
| *Eucrassatella* (*Eucrassatella*) | B | 17 |
| *Strioterebrum* | G | 17 |
| *Haustellum* | G | 15 |
| turbonilline | G | 14 |
| *Lunarca* ? | B | 13 |
| *Parvilucina* (s.l.) | B | 12 |
| *Ondina* | G | 11 |
| *Dendostrea* | B | 11 |
| *Alabina* | G | 11 |
| *Eulimastoma* | G | 11 |
| *Petaloconchus* | G | 10 |
| *Lirophora* | B | 10 |

24. Cayo Agua: Southeast Pt Nispero (Bocas del Toro Basin). PPP: 307, 308, 310, 311, 313, 476.

| Genus and subgenus | Class | Number of Specimens |
|---|---|---|
| *Varicorbula* | B | 1494 |
| *Tucetona* | B | 242 |
| *Caryocorbula* | B | 215 |
| *Crassinella* | B | 168 |
| *Argopecten* | B | 110 |
| *Gouldia* | B | 77 |
| *Alabina* | G | 49 |
| *Ringicula* (*Ringiculella*) | G | 39 |
| *Alvania* | G | 34 |
| *Chama* | B | 32 |
| *Petaloconchus* | G | 31 |
| *Acteocina* | G | 27 |
| turbonilline | G | 26 |
| *Volvulella* (*Volvulella*) | G | 23 |
| *Sulcoretusa* | G | 21 |
| *Meioceras* | G | 21 |
| *Strombus* | G | 20 |
| *Turritella* | G | 20 |
| *Anadara* (*Rasia*) | B | 20 |
| *Cyclopecten* | B | 19 |
| *Cavolinia* | G | 19 |
| marginellid | G | 18 |
| *Parvilucina* (s.l.) | B | 18 |
| *Tellidorella* | B | 17 |
| *Conus* | G | 16 |
| *Natica* (*Naticarius*) | G | 16 |

25. Isla Popa (Bocas del Toro Basin). PPP: 422, 426, 427, 1276, 1277, 1283, 1284.

| Genus and subgenus | Class | Number of Specimens |
|---|---|---|
| *Varicorbula* | B | 1498 |
| *Caryocorbula* | B | 174 |
| *Tucetona* | B | 116 |
| *Meioceras* | G | 86 |
| *Alabina* | G | 48 |
| *Lirophora* | B | 33 |
| *Gouldia* | B | 27 |
| *Fissidentalium* | S | 26 |
| *Macrocallista* (*Megapitaria*) | B | 24 |

APPENDIX 3.—Continued.

| Genus and subgenus | Class | Number of Specimens |
|---|---|---|
| *Saccella* | B | 23 |
| *Oliva (Oliva)* | G | 23 |
| *Stigmaulax* | G | 22 |
| *Trigoniocardia* (s.l.) | B | 22 |
| *Argopecten* | B | 21 |
| *Conus* | G | 19 |
| *Petaloconchus* | G | 16 |
| *Polystira* | G | 14 |
| *Crenella* | B | 14 |
| *Eucrassatella (Eucrassatella)* | B | 12 |
| *Prunum* | G | 11 |
| *Anomia* | B | 11 |
| *Arcinella* | B | 9 |
| *Lucina (Lepilucina)* | B | 9 |
| *Dendostrea* ? | B | 8 |
| *Cadulus* | S | 8 |
| *Strombus* | G | 8 |
| *Voluta* | G | 8 |
| 26. Cayo Agua: Pt Norte East (Bocas del Toro Basin). PPP: 200, 201, 217, 373, 475, 1203. | | |
| *Antillophos (Antillophos)* | G | 538 |
| *Anadara (Rasia)* | B | 296 |
| *Turritella* | G | 143 |
| *Polystira* | G | 106 |
| *Conus* | G | 103 |
| *Strioterebrum* | G | 79 |
| *Hindsiclava* | G | 78 |
| *Prunum* | G | 76 |
| *Cancellaria* (s.l.) | G | 66 |
| *Sconsia* | G | 58 |
| *Petaloconchus* | G | 57 |
| *Stigmaulax* | G | 47 |
| *Oliva (Oliva)* | G | 44 |
| *Crassinella* | B | 44 |
| *Voluta* | G | 36 |
| *Serpulorbis* | G | 24 |
| *Solenosteira* | G | 23 |
| *Strombus* | G | 19 |
| *Tucetona* | B | 18 |
| *Olivella (Macgintiella)* | G | 14 |
| *Argopecten* | B | 14 |
| *Lirophora* | B | 13 |
| *Fasciolaria (Fasciolaria)* | G | 11 |
| *Architectonica* | G | 11 |
| *Calliostoma* | G | 10 |
| 27. Cayo Agua: Pt. Piedra Roja West (Bocas del Toro Basin). PPP: 204, 345, 346, 348, 350, 1188. | | |
| *Varicorbula* | B | 870 |
| *Tucetona* | B | 569 |
| *Caryocorbula* | B | 528 |
| *Alabina* | G | 449 |
| *Argopecten* | B | 440 |
| *Crassinella* | B | 229 |
| *Acteocina* | G | 186 |
| *Gouldia* | B | 183 |
| *Anadara (Rasia)* | B | 168 |
| *Oliva (Oliva)* | G | 160 |
| *Strombus* | G | 156 |
| *Turritella* | G | 151 |
| *Moerella* | B | 139 |
| *Macrocallista (Megapitaria)* | B | 97 |
| *Cadulus* | S | 94 |
| *Hyotissa* | B | 94 |
| *Ringicula (Ringiculella)* | G | 90 |
| carditesine | B | 70 |
| *Conus* | G | 65 |
| *Cyclopecten* | B | 56 |
| *Natica* | G | 55 |
| *Dentalium* (s.l.) | S | 53 |
| *Trachycardium (Phlogocardia)* | B | 48 |
| *Spondylus* | B | 45 |
| caecid | G | 45 |
| *Crenella* | B | 45 |
| 28. Quebrada Brazo Seco (Limon Basin). PPP: 1775, 1776, 1777. | | |
| *Varicorbula* | B | 37 |
| *Turritella* | G | 33 |
| *Caryocorbula* | B | 20 |
| *Volvarina* | G | 9 |
| *Natica (Naticarius)* | G | 8 |
| *Stigmaulax* | G | 7 |
| pyramidelline | G | 7 |
| *Dentimargo* | G | 7 |
| *Ancilla (Eburna)* | G | 6 |
| *Lirophora* | B | 5 |
| *Marginella* | G | 5 |
| *Strombinophos* | G | 5 |
| *Natica* | G | 5 |
| *Dendostrea* ? | B | 5 |
| *Olivella (Dactylidella)* | G | 5 |
| *Prunum* | G | 4 |
| *Anomia* | B | 4 |
| *Persicula* | G | 3 |
| *Polystira* | G | 3 |
| *Kurtziella (Cryoturris)* | G | 3 |
| *Saccella* | B | 3 |
| *Kurtziella (Kurtziella)* | G | 3 |
| *Sincola (Sinaxila)* | G | 3 |
| *Sincola (Sincola)* | G | 3 |
| *Solariella* | G | 3 |
| *Nassarius* (s.l.) | G | 3 |
| *Volvulella (Volvulella)* | G | 3 |
| *Olivella (Macgintiella)* | G | 3 |
| 29. Shark Hole Point (Bocas del Toro Basin). PPP: 390, 391, 392, 396, 1976, 1977, 1978. | | |
| *Fissidentalium* | S | 119 |
| *Amarophos* | G | 75 |
| *Polystira* | G | 41 |
| *Argopecten* | B | 36 |
| *Volvarina* | G | 19 |
| *Stigmaulax* | G | 17 |
| *Bathygalea (Miogalea)* | G | 11 |
| *Conus* | G | 9 |
| turrid | G | 8 |
| *Oliva (Oliva)* | G | 7 |
| *Natica (Naticarius)* | G | 6 |
| *Antillophos (Antillophos)* | G | 4 |
| *Polinices* | G | 4 |

APPENDIX 3.—Continued.

| Genus and subgenus | Class | Number of Specimens |
|---|---|---|
| *Anadara* (*Rasia*) | B | 4 |
| *Homalopoma* (*Leptothyropsis*) | G | 4 |
| *Carinodrillia* | G | 4 |
| *Compsodrillia* | G | 3 |
| *Saccella* | B | 3 |
| *Crucibulum* (*Crucibulum*) | G | 3 |
| *Strioterebrum* | G | 3 |
| *Fusiturricula* | G | 3 |
| *Anomia* | B | 3 |
| typhine | G | 3 |
| *Miraclathurella* | G | 3 |
| *Natica* (*Natica*) ? | G | 2 |
| *Agladrillia* (*Agladrillia*) | G | 2 |
| *Architectonica* | G | 2 |
| *Cancellaria* (s.l.) | G | 2 |
| *Macrocallista* (*Megapitaria*) | B | 2 |
| 30. Finger Island (Bocas del Toro Basin). PPP: 191, 477, 1996. | | |
| *Conus* | G | 231 |
| *Tellidorella* | B | 172 |
| *Polystira* | G | 156 |
| *Strioterebrum* | G | 79 |
| *Subcancilla* | G | 50 |
| *Tesseracme* | S | 49 |
| *Dentalium* (s.l.) | S | 49 |
| *Cancellaria* (s.l.) | G | 47 |
| *Sconsia* | G | 46 |
| *Ervilia* | B | 36 |
| *Scobinella* | G | 36 |
| *Crassinella* | B | 35 |
| *Natica* (*Naticarius*) | G | 34 |
| *Saccella* | B | 33 |
| *Ficus* | G | 33 |
| *Hindsiclava* | G | 31 |
| *Anadara* (*Rasia*) | B | 31 |
| *Syntomodrillia* | G | 29 |
| *Antillophos* (*Antillophos*) | G | 29 |
| *Architectonica* | G | 28 |
| *Acila* | B | 25 |
| *Carinodrillia* | G | 21 |
| *Polinices* | G | 19 |
| *Antillophos* (*Antillophos*) ? | G | 18 |
| *Linga* (*Pleurolucina*) | B | 17 |
| *Solenosteira* | G | 17 |
| 31. Rio Sand Box and Hone Creek (Limon Basin). PPP: 453, 454, 1736, 1737, 1774, 1989. | | |
| *Turritella* | G | 295 |
| *Strombina* (*Strombina*) ? | G | 33 |
| *Polystira* | G | 32 |
| *Olivella* (*Macgintiella*) | G | 29 |
| *Sconsia* | G | 28 |
| *Natica* | G | 24 |
| *Antillophos* (*Antillophos*) | G | 24 |
| *Nassarius* (s.l.) | G | 21 |
| *Acila* | B | 20 |
| *Cadulus* | S | 14 |
| *Oliva* (*Oliva*) | G | 13 |
| *Polinices* | G | 13 |
| turrid | G | 11 |
| *Natica* (*Naticarius*) | G | 11 |
| *Strombinophos* | G | 9 |
| *Volvarina* ? | G | 9 |
| *Cancellaria* (s.l.) | G | 9 |
| *Prunum* | G | 7 |
| *Conus* | G | 7 |
| *Caryocorbula* | B | 6 |
| *Terebra* | G | 6 |
| *Voluta* | G | 6 |
| *Microgaza* ? | G | 6 |
| *Dentalium* (s.l.) | S | 5 |
| *Chiodrillia* ? | G | 4 |
| 32. Rio Tuba (Limon Basin). PPP: 1765, 1766, 1768, 1769, 1770. | | |
| scaphopod | S | 11 |
| *Teinostoma* | G | 8 |
| turbonilline | G | 5 |
| *Cadulus* | S | 5 |
| pyramidelline | G | 4 |
| *Fissidentalium* | S | 4 |
| *Subcancilla* | G | 4 |
| *Dentalium* (s.l.) | S | 4 |
| *Eulimastoma* ? | G | 3 |
| *Meioceras* | G | 3 |
| *Natica* (*Naticarius*) | G | 3 |
| *Saccella* | B | 3 |
| *Turritella* | G | 2 |
| caecid | G | 2 |
| *Acteocina* | G | 2 |
| *Polinices* | G | 2 |
| *Prunum* | G | 2 |
| *Arcinella* | B | 2 |
| *Dentimargo* | G | 1 |
| *Tucetona* | B | 1 |
| *Cyclostremiscus* (*Ponocyclus*) | G | 1 |
| *Cosmioconcha* | G | 1 |
| triphorid | G | 1 |
| *Varicorbula* | B | 1 |
| *Macrocallista* (*Megapitaria*) | B | 1 |
| *Balcis* | G | 1 |
| *Bellaspira* | G | 1 |
| *Antillophos* ? | G | 1 |
| *Volvulella* (*Volvulella*) | G | 1 |
| *Argopecten* ? | B | 1 |
| *Alabina* | G | 1 |
| *Architectonica* | G | 1 |
| *Chama* | B | 1 |
| *Carinodrillia* | G | 1 |
| *Eurytellina* | B | 1 |
| *Cancellaria* (s.l.) | G | 1 |
| *Strioterebrum* | G | 1 |
| *Agladrillia* ? | G | 1 |
| *Lamelliconcha* | B | 1 |
| *Oliva* (*Oliva*) | G | 1 |
| 33. Rio Calzones (North Coast). PPP: 162, 163. | | |
| *Argopecten* | B | 54 |
| *Tucetona* | B | 37 |
| *Ervilia* | B | 19 |
| *Flabellipecten* | B | 8 |
| *Axinactis* (*Glycymerella*) | B | 6 |

APPENDIX 3.—Continued.

| Genus and subgenus | Class | Number of Specimens |
|---|---|---|
| *Acteocina* | G | 4 |
| *Nucula* (*Nucula*) | B | 4 |
| *Gouldia* | B | 3 |
| *Conus* | G | 3 |
| *Parvilucina* (s.l.) | B | 3 |
| *Eucrassatella* (*Eucrassatella*) | B | 3 |
| *Architectonica* | G | 2 |
| *Vitrinella* ? | G | 2 |
| *Irus* (*Irus*) ? | B | 2 |
| *Terebra* | G | 2 |
| *Crassinella* | B | 2 |
| *Oliva* (*Oliva*) | G | 2 |
| *Solariella* | G | 2 |
| *Spondylus* | B | 2 |
| *Transennella* | B | 1 |
| neogastropod | G | 1 |
| *Calliostoma* ? | G | 1 |
| *Cantharus* | G | 1 |
| *Cyclopecten* | B | 1 |
| *Alabina* | G | 1 |
| naticid | G | 1 |
| *Macrocallista* (*Megapitaria*) | B | 1 |
| *Tricolia* | G | 1 |
| *Chama* | B | 1 |
| *Hiatella* ? | B | 1 |
| *Polystira* | G | 1 |
| *Anomia* | B | 1 |
| *Petaloconchus* | G | 1 |
| carditesine | B | 1 |
| *Meioceras* | G | 1 |
| corbulid | B | 1 |
| *Hyotissa* | B | 1 |
| *Ringicula* (*Ringiculella*) ? | G | 1 |
| *Lirophora* | B | 1 |
| eulimid | G | 1 |
| muricid ? | G | 1 |
| 34. Miguel de la Borda (North Coast). PPP: 1973. | | |
| *Crassinella* | B | 75 |
| *Varicorbula* | B | 72 |
| *Saccella* | B | 44 |
| *Lirophora* | B | 43 |
| *Nassarius* (s.l.) | G | 34 |
| caecid | G | 30 |
| *Eurytellina* ? | B | 26 |
| *Parvilucina* (s.l.) | B | 21 |
| *Macrocallista* (*Megapitaria*) | B | 19 |
| *Natica* (*Naticarius*) | G | 17 |
| *Caryocorbula* | B | 16 |
| *Cadulus* | S | 15 |
| *Anadara* (s.l.) | B | 15 |
| *Acteocina* | G | 15 |
| *Tellina* (*Scissula*) | B | 15 |
| *Lamelliconcha* | B | 15 |
| *Acila* | B | 14 |
| *Turritella* | G | 13 |
| *Crepidula* | G | 10 |
| eulimid | G | 9 |
| *Cylichnella* | G | 9 |
| *Oliva* (*Oliva*) | G | 8 |
| *Gadilopsis* | S | 7 |
| *Atrina* | B | 7 |
| *Anadara* (*Rasia*) | B | 6 |
| *Mitrella* | G | 6 |
| *Cyclostremiscus* (*Ponocyclus*) | G | 6 |
| 25. Isla Payardi (Panama Canal Basin). PPP: 34, 225, 226, 487, 488, 489, 1077, 1079, 1080, 1081, 1086, 1087, 1307, 1308. | | |
| *Turritella* | G | 3136 |
| *Anadara* (*Rasia*) | B | 1661 |
| *Lirophora* | B | 1069 |
| *Strombina* (*Strombina*) | G | 1048 |
| *Oliva* (*Oliva*) | G | 800 |
| *Cadulus* | S | 676 |
| *Antillophos* (*Antillophos*) | G | 483 |
| *Cancellaria* (s.l.) | G | 448 |
| *Conus* | G | 386 |
| *Chama* | B | 365 |
| *Hyotissa* | B | 356 |
| *Natica* (*Naticarius*) | G | 344 |
| *Polinices* | G | 324 |
| *Polystira* | G | 284 |
| *Architectonica* | G | 253 |
| *Olivella* (*Niteoliva*) | G | 225 |
| *Stigmaulax* | G | 208 |
| *Petaloconchus* | G | 184 |
| *Nassarius* (s.l.) | G | 154 |
| *Strioterebrum* | G | 145 |
| *Ervilia* | B | 132 |
| *Caryocorbula* | B | 132 |
| *Cylichnella* | G | 128 |
| *Terebra* (*Panaterebra*) | G | 110 |
| *Flabellipecten* | B | 83 |
| 36. Mattress Factory (Panama Canal Basin). PPP: 224, 227, 229, 230, 484, 485, 486, 1030, 1031, 1032, 1033, 1034, 1035, 1078, 1305, 1306. | | |
| *Turritella* | G | 1523 |
| *Ervilia* | B | 1470 |
| *Cymatophos* | G | 949 |
| *Alabina* | G | 526 |
| *Alveinus* | B | 487 |
| *Olivella* (*Niteoliva*) | G | 471 |
| *Polinices* | G | 447 |
| *Strioterebrum* | G | 423 |
| *Cadulus* | S | 385 |
| *Nassarius* (s.l.) | G | 280 |
| *Anadara* (*Rasia*) | B | 268 |
| *Cancellaria* (s.l.) | G | 259 |
| *Stigmaulax* | G | 212 |
| *Leptopecten* | B | 194 |
| *Caryocorbula* | B | 187 |
| *Oliva* (*Oliva*) | G | 163 |
| *Trigoniocardia* (s.l.) | B | 145 |
| *Cylichnella* | G | 144 |
| *Anadara* (*Cunearca*) | B | 140 |
| *Natica* (*Naticarius*) | G | 138 |
| *Acteocina* | G | 138 |
| *Strombina* (*Strombina*) | G | 136 |
| *Eucrassatella* (*Hybolophus*) | B | 134 |

APPENDIX 3.—Continued.

| Genus and subgenus | Class | Number of Specimens |
|---|---|---|
| *Crassinella* | B | 117 |
| *Crucibulum* (*Crucibulum*) | G | 105 |
| 37. Martin Luther King (Panama Canal Basin). PPP: 218, 219, 220, 221, 222, 223, 231, 232, 233, 490, 1075. | | |
| *Cymatophos* | G | 2124 |
| *Turritella* | G | 1022 |
| *Strioterebrum* | G | 467 |
| *Cancellaria* (s.l.) | G | 435 |
| *Olivella* (*Niteoliva*) | G | 420 |
| *Ervilia* | B | 318 |
| *Trigoniocardia* (s.l.) | B | 314 |
| *Polinices* | G | 286 |
| *Anadara* (*Rasia*) | B | 264 |
| *Crassinella* | B | 245 |
| *Architectonica* | G | 234 |
| *Macrocallista* (*Megapitaria*) | B | 210 |
| *Natica* (*Naticarius*) | G | 206 |
| *Caryocorbula* | B | 184 |
| *Leptopecten* | B | 181 |
| *Oliva* (*Oliva*) | G | 166 |
| *Conus* | G | 146 |
| *Nassarius* (s.l.) | G | 133 |
| *Eupleura* | G | 111 |
| *Cadulus* | S | 101 |
| *Solenosteira* | G | 87 |
| *Agladrillia* (*Agladrillia*) | G | 76 |
| *Semele* | B | 76 |
| *Chionopsis* | B | 70 |
| *Neverita* (*Glossaulax*) | G | 66 |

# CHAPTER 10

# NEOGENE-QUATERNARY OSTRACODA AND PALEOENVIRONMENTS OF THE LIMON BASIN, COSTA RICA, AND BOCAS DEL TORO BASIN, PANAMA

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## INTRODUCTION

Tropical marine ostracodes from Neogene and Quaternary sediments of the Central American Caribbean region have been the subject of biostratigraphic (Bold, 1988), ecological (Krutak, 1971), taxonomic (Teeter, 1975), and evolutionary studies (Cronin, 1988; Cronin and Schmidt, 1988). As part of the Panama Paleontology Project (PPP), Neogene and Quaternary ostracodes are being studied from the Central American region. The overall goal of this research is to evaluate the impact of the emergence of the Central American Isthmus as a land barrier between the Caribbean/tropical Atlantic and the Pacific oceans on marine ostracode biodiversity and the oceanic environments in which extant ostracodes evolved. Due to the ecological specificity of many living tropical ostracode species, they are ideally suited for reconstructing paleoenvironments on the basis of their occurrence in fossil assemblages, which in turn can lead to a better understanding of the tropical climatic and tectonic history of Central America.

The principal aims of this chapter are: (a) to document the composition of the ostracode assemblages from the Limon Basin of Costa Rica and the Bocas del Toro Basin of Panama, two areas yielding extensive marine ostracode assemblages; (b) to describe the environments of deposition within these basins; and (c) to document the stratigraphic distribution of potentially age-diagnostic ostracode species in the Limon and Bocas del Toro basins in order to enhance their use in Central American biostratigraphy. A secondary, but none-the-less important goal is to assemble a database on the distribution of modern ostracode species in the Caribbean and adjacent areas as a basis for comparison with fossil assemblages. Although the ecological, biostratigraphic and paleoenvironmental conclusions presented here will improve as additional material is studied, these fossil and modern ostracode databases constitute the foundation for future evolutionary and geochemical studies of tropical Caribbean and eastern Pacific Ocean ostracodes. Moreover, we present here evidence that major faunal and oceanic changes occurred in the western Caribbean over the last 4 million years, probably related to changes in ocean circulation due to the emergence of the Isthmus as well as other climatic events.

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Table 1.—Limon Basin, Costa Rica, and Bocas del Toro Basin, Panama, PPP samples used herein. Section numbers and names from Appendix B.

| Samples (PPP numbers) | Formation | Section |
|---|---|---|
| 59–62, 293, 298, 300, 306, 307, 334, 335, 337, 371–374 | Cayo Agua | 19. North Point to Tiburon Point |
| 63 | Cayo Agua | 16. North Point, Western Side |
| 168–169 | Escudo de Veraguas | 11. Southeastern Coast |
| 175, 358, 360–369 | Escudo de Veraguas | 10. Northern Coast |
| 389 | Shark Hole Point | 12. Bruno Bluff to Plantain Cays, Valiente Peninsula |
| 410 | Nancy Point | 12. Bruno Bluff to Plantain Cays, Valiente Peninsula |
| 634–638, 645, 953–955, 959–960, 1480–1483 | Moin | 36. Lomas del Mar, Eastern Sequence |
| 647–658, 1357, 1375–1376, | Moin | 37. Lomas del Mar, Western Reef Flank Sequence |
| 668, 670, 672, 678, 679, 682–684, 685–688, 690 | Rio Banano | 29. Rio Banano |
| 710 | Moin | * Los Laureles |
| 712, 1369–1371, 1392–1406, 1435, 1436, 1438, 1442, 2003 | Moin | 34. Empalme |
| 720–721 | Moin | 32. Santa Rita |
| 1433–1434 | Moin | * Avenida Barracuda |

* = isolated outcrop.

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## MATERIAL AND METHODS

Table 1 lists the formations, section names, and sample numbers associated with each outcrop section that we studied for ostracodes. Sample numbers are keyed to the Panama Paleontology Project Database described by Kaufmann and Fortunato (this volume). Most samples described here were taken for ostracode study and were processed and/or picked for ostracodes at the U. S. Geological Survey in Reston, Virginia, or the Department of Geology and Geophysics, Louisiana State University, Baton Rouge, Louisiana. We processed sediment first by soaking 50-gram (dry weight) samples for one to two days in water in which a small amount of sodium bicarbonate had been dissolved. In rare cases, we disaggregated sediment using Varsol. Sediment was then washed through a 63 μm sieve and the size fraction greater than 150 μm was picked for ostracodes. Because of the large number of samples, we focused on key sections from each region to obtain data on the preservation, abundance and diversity of the assemblages. In most cases, samples were completely picked of ostracodes; abundances ranged from seven to 1501 valves, with an average of 229 valves in 104 samples. In samples where ostracodes were present in great numbers, standard micro-splitting techniques were used so that at least 200–300 individual valves were obtained in order to perform quantitative analyses of assemblages.

Table 2 contains fossil ostracode census data considered in this chapter. Because the study of the taxonomy of tropical marine ostracodes from the Central American Caribbean region is uneven, the taxonomic categories used in our analyses reflect this unevenness in that we were obliged to use both genus- and species-level categories in the census data. Figured specimens shown in Plates 1, 2 and 3, have been reposited at the United States National Museum of Natural History. A large modern ostracode database was assembled in order to provide a basis for paleoenvironmental interpretations. The fossil and modern databases are available electronically from the first author and the fossil data are at http://www.fiu.edu/˜collinsl/.

Two sets of semi-quantitative cluster analyses were executed using presence-absence data: one analysis of 57 Moin Formation samples using 41 taxa and a second set of analyses of 44 taxa from selected samples from the Limon and Bocas del Toro Basins. The Jaccard coefficient provides a commonly used binary coefficient that tends to slightly emphasize the differences between two assemblages more than some other coefficients (Cheetham and Hazel, 1969). We used presence-absence as opposed to relative abundances because the wide variation in ostracode abundance in samples from different lithologies makes it unattractive to compare samples using species proportions. Second, the specific ecology of many tropical ostracode species is such that dominant species characterize one or two of the tropical biofacies encountered. Jaccard coefficients were calculated for the presence-absence matrix and a cluster analysis of the resulting matrix was performed using the average linkage method (Text-fig. 1) and complete linkage method (Text-fig. 2a and 2b).

## MODERN OSTRACODES FROM THE CARIBBEAN SEA

Maddocks (1974) and Bold (1983, 1988) give excellent comprehensive introductions to the taxonomy, ecology and biostratigraphy of Caribbean ostracodes. Our goal was to construct from the large but scattered and somewhat uneven literature a database (Modern Ostracode Database) on modern ostracode ecology and zoogeography for species living in the tropical seas of the Caribbean and adjacent regions. This database provides a reasonable basis for making paleoenvironmental inferences from fossil assemblages occurring in the Central American region. We chose to include selected species and/or generic census data from five primary sources (Cronin and Dowsett, 1990; Fithian, 1980; Kontrovitz, 1976; Krutak, 1982; Teeter, 1975) for three reasons. First, they all provided excellent illustrations or references to illustrations, allowing taxonomic consistency across different geographical areas. Secondly, they span a wide spectrum of ecological habitats, from restricted lagoons to the continental slope, and include all biofacies encountered in Neogene and Quaternary sediments. Finally, each reference contains species census counts (not just presence/absence data) that give us information on the relative frequency of dominant and rare taxa and which will allow future quantitative comparisons between fossil and Recent assemblages. It is important to emphasize that the paleoenvironmental reconstructions given below for Neogene and Pleistocene ostracode biofacies are based heavily on the ecological data contained in the Modern Ostracode Database, deemed adequate for reconstructing past environments of deposition.

## OSTRACODES FROM LIMON BASIN, COSTA RICA

Ostracode species occurrence data for the Moin and Rio Banano formations of the Limon Basin and for the Bocas del Toro Basin are given in Table 2. The following are short summaries of the ostracodes from each formation and the environmental significance of the biofacies.

### MOIN FORMATION

We identified ostracode biofacies in the Moin Formation, Limon Basin, to determine the late Pliocene-early Pleistocene environmental history of the region and to provide regional biostratigraphic correlation between the Limon and the Bocas del Toro basins. The lithostratigraphy followed here is based on work by Taylor (1975), Cassell and Sen Gupta (1989), Coates *et al.* (1992), and Coates (this volume). The Moin Formation consists of several distinct lithofacies and macrofaunal biofacies, most notably a fine-grained facies (originally described from an unnamed creek that flows through the Cangrejos community) and a coral reef facies (Appendix A, Map 11, Inset B). There appear to be at least three distinct coral reef trends in the region of the city of Limon (Taylor, 1975; McNeill *et al.*, 1996; McNeill *et al.*, in press; Budd *et al.*, this volume). Although the stratigraphic relationships between the Cangrejos creek and reefal facies are not yet firmly established, we were able to distinguish the youngest trend from the older trends on the basis of the ostracode assemblages and provide a preliminary interpretation of their significance. We were also able to make a preliminary comparison to ostracode assemblages from the Quebrada Chocolate section (Appendix A, Map 11, Inset A; associated with the oldest trend and now considered part of the Quebrada Chocolate Formation).

A total of 57 samples from two measured sections (Cangrejos creek and Lomas del Mar) and several smaller exposures of the Moin Formation, and one measured section (CTA Fence) currently considered part of the Rio Banano Formation (Appendix A, Map 11, Inset C) form the basis of this analysis (Table 1, 2). The cluster analysis of the ostracode data (57 samples, 41 taxa; Text-fig. 1) revealed five groups of samples, A–E, referred to here as biofacies (Hazel, 1971, 1988), each being characteristic of a faunal assemblage and indicative of distinct environments of deposition.

#### *Biofacies A*

This biofacies is represented by Cluster A (Text-fig. 1) and consists of 12 samples, nine of which come from the type section of the Moin Formation exposed along Cangrejos creek west of the city of Limon. The dominant taxa in order of their mean percentage occurrence in a sample are: *Krithe* spp. (12%), *Cytheropteron wardensis* Puri, 1954 (12%), *Argilloecia* spp. (14%), *Bradleya* aff. *B. acceptabilis* Lübimova and Sánchez-Arango, 1974 (7%), *Loxocorniculum* spp. (6%). Other taxa averaging 5% include *Radimella confragosa* (Edwards, 1944), *Cytherella* spp. and *Echinocythereis madremastrae* Bold, 1988. *Bradleya* aff. *B. acceptabilis* is closely related to the living species *B. normani* (Brady, 1866), which Bold (1968) suggested inhabits the Caribbean today.

This biofacies represents a mixture of shallow, warm-water, carbonate-platform taxa (*Loxocorniculum,* and to a lesser extent, *Radimella*), taxa typical of outer shelf/upper slope, cooler-water habitats in the Atlantic/Caribbean (*Cytherella, Echinocythereis*), and typically deep colder-water taxa (*Krithe, Bradleya*). *Krithe* is the predominant genus in the world's deep-sea environments (Coles *et al.,* 1994; Van Harten, 1996), usually comprising 40–70% of assemblages in

Table 2.—Ostracode census data by PPP number from the Limon Basin, Costa Rica, and Bocas del Toro Basin, Panama. Data are available at internet site http://www.fiu.edu/~collinsl/.

| Taxon no | Taxa | 59 | 60 | 61 | 62 | 63 | 168 | 169 | 175 | 293 | 298 | 300 | 306 | 307 | 334 | 335 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | *Actinocythereis gomillionensis* (Howe and Ellis, 1935) | | | | | | | | | | | | | | | |
| 2 | *Ambocythere* spp. | | 3 | | 1 | | | 1 | 1 | | | | | | | |
| 3 | *Argilloecia* spp. | | | 3 | | | 2 | 4 | | | | | | | | |
| 4 | *Aurila* spp. | | | | | | | 11 | 4 | | 5 | | | | | |
| 5 | Bairdiids | | | | | | 13 | | 53 | | 1 | 1 | | 1 | | 4 |
| 6 | *Bairdoppilata* spp. | | | | | | | | | | | | | | | |
| 7 | *Basslerites* cf *B. minutus* | 17 | | | | | | | | | | | | | | |
| 8 | *Basslerites minutus* Bold, 1953 | | 1 | 2 | | | | 1 | | | 3 | | | | 12 | 1 |
| 9 | *Basslerites* sp. | | | | 2 | | | | | 3 | 4 | 3 | | 4 | 2 | |
| 10 | *Bradleya* aff. *B. acceptabilis* Lubimova and Sanchez-Arango, 1974 | | | | | | 6 | 10 | | | | | | | | |
| 11 | Buntonids | | | | | | | | | | | | | | | |
| 12 | *Bythoceratina* spp. | | | | | | 1 | 3 | | | | | | 1 | | |
| 13 | *Caribbella puseyi* Teeter, 1975 | | | | 24 | | | | | | | | | | | |
| 14 | *Cativella* sp. | | | | | | | | | | | | | | | |
| 15 | *Cativella navis* Coryell and Fields, 1937 | 19 | 18 | 8 | 7 | 5 | 24 | 26 | 16 | | 4 | | 1 | 1 | 5 | 7 |
| 16 | *Cativella pulleyi* Teeter, 1975 | | | 9 | | 27 | | | | | | | | | | |
| 17 | *Caudites* aff. *C. rectangularis* (Brady, 1869) | | | | | | | | | | | | | | | |
| 18 | *Caudites* aff. *C. highi* Teeter, 1975 | | | | | | | | | | | | | | | |
| 19 | *Caudites medialis* Coryell and Fields, 1937 | 2 | 1 | 5 | | | | | 5 | 1 | 2 | 1 | | | 4 | |
| 20 | *Caudites nipeensis* Bold, 1946 | | | | 35 | | | 5 | | | 3 | | | 6 | | 4 |
| 21 | *Caudites symmetricus* Bate, Whittaker and Mayes, 1981 | | | | | | | | | | | | | | | |
| 22 | *Caudites* spp. | | | | 3 | | 1 | 20 | 5 | 1 | | | | | 1 | 1 |
| 23 | *Coquimba fissispinata* Benson and Coleman, 1963 | | | | | | | | | | | | | | | |
| 24 | *Costa stokesae* Bold, 1967 | | | | | | 1 | 4 | | | | | | | | |
| 25 | *Cushmanidea* sp. | | | | | | 1 | | | | | | | | | |
| 26 | *Cytherella* spp. | 12 | 30 | 6 | 27 | 12 | 10 | 25 | 14 | 2 | 15 | 16 | | | 6 | 6 |
| 27 | *Cytherelloidea* spp. | 1 | | 1 | | 6 | 2 | 3 | 6 | 1 | | 1 | | | | |
| 28 | *Cytheropteron* spp. | 3 | | 23 | 16 | 54 | 15 | 24 | 4 | | 45 | 7 | | 1 | 4 | 27 |
| 29 | *Cytheropteron (Lobosocytheropteron) palton* Bold, 1966 | | | | 1 | | | 1 | | | | 2 | | 5 | 1 | 9 |
| 30 | *Cytherura* spp. | | 41 | 2 | 7 | | 1 | | 11 | 2 | 5 | 3 | | 5 | 1 | 3 |
| 31 | *Echinocythereis madremastrae* Bold, 1988 | | | | | | | | | | | | | | | 4 |
| 32 | *Eucytherura* spp. | | | | | | | 3 | | | 1 | 1 | | | | |
| 33 | *Gangamocytheridea plicata* Bold, 1968 | | | | | | | | | | | | | | | |
| 34 | *Heinia* spp. | | | 1 | | | | | 2 | | | | | | | |
| 35 | *Hemicytherura* spp. | | | | | | | | | | | | | | | |
| 36 | *Hermanites hornbrooki* (Puri, 1960) | | | | | | | | | | | | | | | |
| 37 | *Hulingsina* spp. | 2 | | | | | 1 | | 1 | 2 | 2 | 3 | | 45 | | 2 |
| 38 | *Jonesia* sp. | | | | | | 1 | 2 | 2 | | | | | | | |
| 39 | *Jugosocythereis pannosa* (Brady, 1869) | | | | | | 1 | | 3 | | 1 | | | | | |
| 40 | *Kangarina* spp. | | | | | | | 3 | 1 | | | 2 | | | | |
| 41 | *Krithe* spp. | | | 1 | | 5 | 1 | 6 | 6 | | | | | | | |
| 42 | *Loxoconcha* spp. | 3 | | 2 | 2 | 4 | | | | 5 | 8 | 10 | | | 7 | |
| 43 | *Loxocorniculum* spp. | 2 | | 2 | 20 | | 5 | 23 | 48 | 32 | 149 | 48 | 2 | 31 | 30 | 144 |
| 44 | Macrocyprids | | 2 | | | | 4 | 9 | 2 | | | | | | | |
| 45 | *Megacythere johnsoni* (Mincher, 1941) | | | | | | | | | | | | | | | |
| 46 | *Microcythere* sp. | | | | | | | | | | | | | | | |
| 47 | *Munseyella bermudezi* Bold, 1966 | | | | | | | | | | | | | | | 1 |
| 48 | *Neocaudites scottae* Teeter, 1975 | 4 | 2 | 5 | 15 | | 3 | 17 | 7 | 1 | 17 | 4 | | | 4 | 4 |
| 49 | *Costa* cf. *Costa variabilicostata recticostata* Bold, 1970 | | | | | | 2 | | | | | | | | | |
| 50 | *Occultocythereis angusta* Bold, 1963 | | | | | | | | | | | | | | | |
| 51 | *Orionina boldi* Cronin and Schmidt, 1981 | | | | | | | | | | | | | | | |
| 52 | *Orionina vaughani* (Ulrich and Bassler, 1904) | 3 | | 1 | 10 | | 4 | 11 | 17 | 1 | 1 | 1 | 1 | 1 | | 2 |
| 53 | *Palmoconcha* spp. | | | | | | | | | | | | | | | |
| 54 | Paracyprids | | | | | | 1 | | 10 | | | | | | | |
| 55 | *Paracytheridea* spp. | | | 1 | 16 | | 1 | | 22 | 8 | 21 | 10 | 9 | 20 | 6 | 46 |
| 56 | *Paradoxostoma* spp. | | | | | | | | 12 | 2 | | | | 1 | | 2 |
| 57 | *Parakrithe alta* Bold, 1988 | | | | | | | | | | | | | | | |
| 58 | *Parakrithella* sp. | | | | | | | | | | | | | | | |
| 59 | *Pellucistoma* spp. | 7 | | | 55 | 4 | 1 | | 5 | 11 | 35 | 1 | | 16 | | 1 |
| 60 | *Perissocytheridea* spp. | | | | | | | 2 | 2 | | 4 | | | 1 | 28 | 10 |
| 61 | *Phlyctocythere* spp. | | | | | 1 | | | | | 1 | | | | | |
| 62 | Pontocyprids | | | | | | | | | | | | | | | 7 |
| 63 | Propontocyprids | | | | | | 2 | | 5 | | 3 | | | | | |
| 64 | *Pseudoceratina droogeri* Bold, 1965 | | | | | | | | | | | | | | | |
| 65 | *Pseudocythere caudata* Sars, 1865 | | | | | | | | | | | | | | | |
| 66 | *Pseudosammocythere* spp. | 21 | 7 | 4 | 6 | | 2 | 5 | 12 | 4 | 1 | | | 1 | | |
| 67 | *Pterygocythereis* spp. | | | | 2 | | 3 | | | | 7 | | | | | |
| 68 | *Pumilocytheridea* sp. | 1 | | | 4 | | | 2 | | 1 | 1 | 2 | | 1 | | 1 |
| 69 | *Puriana* spp. | 77 | | 88 | | | | | | | | | | | | |
| 70 | *Reussicythere reussi* (Brady, 1869) | | | | | | | | | | | | | | | |
| 71 | *Quadracythere howei* (Puri, 1953) | | | | | | | | 31 | 5 | 20 | 16 | | 2 | 2 | 10 |
| 72 | *Quadracythere producta* (Brady, 1868) | | | | | | | | 6 | | | | | | | |
| 73 | *Radimella* cf. *R. confragosa* (Edwards, 1944) | | | | | | | | 18 | | | 3 | | | | 8 |
| 74 | *Radimella ovata* Bold, 1988 | | | 10 | 6 | 5 | | | | 5 | 25 | 6 | 1 | 3 | 42 | 15 |
| 75 | *Radimella* aff. *R. ovata* Bold, 1988 | | | | | | 10 | | | | | | | | | |
| 76 | *Radimella wantlandi* (Teeter, 1975) | | | | | | 4 | | 15 | | | | | | | |
| 77 | *Semicytherura* spp. | | | | | | | | | | | | | | | |
| 78 | *Touroconcha lapidiscola* (Hartmann, 1959) | 4 | | 1 | 85 | 2 | 7 | 36 | 28 | 18 | 23 | 3 | | 16 | 3 | 6 |
| 79 | *Triangulocypris laeva* (Puri, 1960) | | | | | | | | | | | | | | | |
| 80 | *Triebelina* spp. | | | | | | 1 | | | | | | | | | |
| 81 | *Uroleberis* sp. | | | | | | | | | | | | | | | |
| 82 | *Xestoleberis* spp. | 18 | 1 | 26 | 3 | 53 | 4 | | 51 | 4 | 17 | 11 | | 2 | 1 | 3 |
| 83 | Ostracode A | | | | | | | | | | | | | | | |
| 84 | Other (unidentified) | | | | | | | | | | | | | | | |
| | Total specimens | 196 | 106 | 201 | 347 | 178 | 135 | 257 | 425 | 109 | 424 | 155 | 14 | 164 | 159 | 328 |

Table 2.—Continued.

| Taxon no. | 337 | 358 | 360 | 361 | 362 | 363 | 364 | 365 | 366 | 367 | 368 | 369 | 371 | 372 | 373 | 374 | 389 | 410 | 634 | 635 | 636 | 638 | 645 | 647 | 648 | 649 | 650 | 651 | 652 | 653 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 2 | | 2 | | 4 | | | 1 | | | | | | | 5 | 7 | 5 | | 1 | | | | | | | | 5 | 7 | 2 | | 1 |
| 3 | | | 7 | 6 | 18 | 9 | 2 | | 2 | 1 | 2 | 2 | | | 1 | | | 1 | | | 4 | 7 | 3 | 31 | 4 | 19 | 83 | 27 | 25 | 2 |
| 4 | | | | | | | | 1 | 1 | | | 1 | | | | | | | | | 2 | | | | | 6 | 7 | 14 | 5 | |
| 5 | 2 | | | 1 | 3 | | | 1 | 3 | 3 | 1 | 2 | | | | | | | 18 | 82 | 50 | 156 | 66 | | 1 | 9 | 16 | 6 | 7 | 1 |
| 6 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 7 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 8 | 5 | | | 1 | | | | | | | | | | 1 | | | | | | | 34 | | | | | | | | | |
| 9 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 10 | | | | | 1 | 1 | | | | 1 | | | | | | | | | | | | 3 | 1 | | 1 | 73 | 23 | 5 | | 34 |
| 11 | | | | | | | | | | | | | | | | | | | | | | | | 6 | | | | | 5 | |
| 12 | | | | | | | | | | | 1 | | | | | | | | | | | 7 | | | | | | | | 4 |
| 13 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 14 | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | |
| 15 | 7 | | | 6 | 2 | 4 | 2 | 3 | | 1 | 12 | | | | | | 2 | | | | | | | | | | | | | |
| 16 | | | | | | | | | | | | | 7 | 10 | 1 | 5 | | | | | | 1 | | | | | | | | 1 |
| 17 | | | | | | | | | | | | | | | | | | | | | 4 | | | | | 13 | 38 | 8 | 16 | 3 |
| 18 | | | | | | | | | | | | | | | | | | | | 2 | | | | | | 1 | 1 | | | |
| 19 | | | | | | | | | | | | | | 2 | | | | | | | | | | | | | | | | |
| 20 | | 3 | | 7 | 3 | 6 | 2 | 8 | 6 | 6 | 1 | 10 | 1 | | | | | | 2 | 7 | 3 | 10 | 5 | | | | | | 2 | 1 |
| 21 | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 22 | 1 | 1 | 2 | 2 | | | | 1 | 4 | | | | | | | | | | | | | | | 4 | | | 6 | 2 | 1 | |
| 23 | | | | | | | 2 | | | | 1 | 1 | | | | | | | 4 | 9 | 5 | | | | | | 2 | | | |
| 24 | | | | | | | | | | | | | | | | | | | | | | 2 | | | 5 | 4 | 1 | | | 1 |
| 25 | | | | | | | | | | | | | | | | | | | | | 13 | | | | | | | | | |
| 26 | 23 | | | 3 | 12 | 1 | | 1 | | 1 | 14 | 5 | 1 | 5 | 1 | 1 | 1 | 6 | | | 1 | 6 | | 9 | 1 | 80 | 14 | | 6 | 5 |
| 27 | | | | | | | | | | | | | | | | | | | 11 | | | 5 | | | | 3 | | | 1 | |
| 28 | 12 | 3 | | 7 | 1 | 6 | | | | 3 | 3 | | 3 | 54 | 1 | | | 1 | | 18 | 5 | 5 | 2 | 2 | 20 | 69 | 48 | 26 | 0 | 6 |
| 29 | 4 | | | 9 | 1 | 2 | 8 | 3 | 3 | 7 | | 7 | | | | | | | | | | | | | 1 | 8 | 12 | 1 | 1 | 3 |
| 30 | 3 | 3 | 3 | | 3 | 5 | | 9 | 8 | | 1 | 3 | | 2 | 1 | 9 | | | 7 | 10 | 24 | 2 | | 2 | 6 | 6 | 4 | 3 | 4 | 2 |
| 31 | | | | | | | | | | | | | | | | | | | | | | | | 8 | | 23 | 10 | 3 | 5 | 36 |
| 32 | | | | 1 | 1 | 1 | | 1 | 2 | 1 | | | | | | | | 1 | | | 2 | 2 | | 2 | 2 | | | | | 1 |
| 33 | | | | | | | | | | | | | | | | | | | | | | 2 | 3 | 1 | | | | | | |
| 34 | | 1 | | | 4 | | | | | | | | | | | | | | | | | | | | 1 | | | | | |
| 35 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 36 | | | | | | | | | | | | | | | | | | | 2 | | | 10 | | 1 | | 1 | | | | 1 |
| 37 | | | | | | | | 5 | | | | 2 | | | | | | | 6 | 7 | 12 | | | | | 1 | | | | |
| 38 | | | | | | | | | | | | | | | | | | | | | 3 | | | | | 1 | 2 | 1 | | 1 |
| 39 | | | | 1 | | | | | | | 1 | | | | | | | | | | 4 | 2 | 3 | | | | 2 | | | |
| 40 | | 1 | 5 | 12 | 2 | 3 | 7 | 11 | 5 | 4 | 2 | 8 | | | | 2 | | 1 | | | 4 | 11 | 7 | 2 | | | | | | |
| 41 | | | 4 | 3 | 2 | | 1 | | | | | | | | | | | 10 | | 2 | | 5 | 4 | 42 | 20 | 49 | 85 | 39 | 11 | 15 |
| 42 | | | | | | 11 | | | | | | 9 | | | | 3 | | | | | 4 | 3 | | 3 | | 1 | 18 | 1 | 5 | 1 |
| 43 | 204 | 5 | | 22 | 5 | 5 | | 16 | 23 | 4 | 3 | 1 | | | | 1 | 1 | | 5 | 12 | 80 | 33 | 22 | 2 | 2 | 22 | 56 | 17 | 16 | 7 |
| 44 | | | | 2 | 4 | 1 | | | | 2 | 1 | | | | | | | | | 24 | 6 | | 9 | 3 | | 3 | | | 4 | 7 |
| 45 | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | |
| 46 | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | |
| 47 | | | | 1 | 2 | 3 | | 1 | | 2 | | | | | | | | 5 | | 4 | | | | 6 | | | 9 | 2 | 5 | 1 |
| 48 | 4 | 3 | | 1 | 8 | 4 | | 1 | 3 | 2 | 9 | 2 | | | | | 1 | | | 10 | 1 | 1 | | | | | 2 | | 1 | |
| 49 | | | | | 1 | | | | | | | | | | | | | | 2 | | 7 | | | | | | 1 | | | 2 |
| 50 | | | | | | | | | | | | | | | | | | | | 1 | 1 | 10 | 6 | | | | | | 1 | |
| 51 | | | | | | | | | | | | | | | | | | | 6 | 3 | | | | | | | 3 | | 1 | |
| 52 | 2 | | | | | | | 1 | | | 2 | 2 | | | | | 1 | | | 13 | 9 | 13 | | | | | | | | |
| 53 | | | | | | | | | | | | | | | | | | | 5 | 3 | 4 | | | | | | | | | 1 |
| 54 | | | | | | | | | | 2 | 5 | | | | | | | | | | 4 | 1 | 2 | | | 5 | 12 | 4 | 5 | 2 |
| 55 | 9 | | 1 | 3 | 3 | 6 | 14 | 4 | 5 | 8 | 6 | 24 | 2 | | 1 | 1 | | | 7 | 13 | 27 | 25 | 7 | 5 | 1 | 8 | 17 | 1 | 6 | 3 |
| 56 | | | | | | | | | 1 | | | | | | | 1 | | | | | | | | | | | 1 | | | |
| 57 | | | | | | | | | | | | | | | | | | | | | | | | 3 | | 6 | 14 | 6 | | |
| 58 | | | | | | | | | | | | | | | | | | | | | | | | | | | 9 | 5 | | |
| 59 | 30 | | | | 2 | 1 | 4 | 5 | 12 | 2 | 2 | | | | | | | | | 1 | 55 | 3 | | | | 1 | | | | |
| 60 | 1 | | | | | 2 | | 1 | | | | | | | | | | | | | 1 | | | | | 2 | 8 | | | |
| 61 | | | 2 | | | | | | | | 1 | | | | | | | | | | 5 | | | | | 4 | 5 | 12 | | 1 |
| 62 | 3 | | | | | | | | | | | | | | | | | | | | 4 | 1 | | 10 | | | | | | |
| 63 | | | | | | | 2 | | | | 1 | | | | | | | | | | 5 | | | | | | 2 | 1 | | |
| 64 | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | |
| 65 | | | | | | | | | 1 | 1 | | | | | | | | | | | | | | | | 3 | | 1 | 2 | |
| 66 | 1 | 1 | 3 | 2 | 4 | 3 | | | 1 | | | | | | 9 | 6 | | | | | | 1 | | 7 | | | | | | |
| 67 | | | 1 | | | | | | | 1 | 1 | 1 | | | | | | | | | | 1 | | | | 9 | 24 | 7 | | 5 |
| 68 | 2 | | | | | | 1 | 2 | 3 | | | 2 | | | | | | | | | | | | | | | | | | |
| 69 | | | | | | | | | | | | | | | 1 | | 8 | | | 10 | 76 | | | | | 2 | | | | |
| 70 | | | | | | | | | | | | | | | | | | | | | 71 | | | | | | | | | |
| 71 | 7 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | |
| 72 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 73 | | | | | | | | | | | | | | 1 | | | | | 16 | 24 | 17 | 37 | 112 | 3 | | 22 | 26 | 11 | 23 | 4 |
| 74 | 2 | 8 | | | | | | | | | | 13 | | | | | | | 11 | 85 | | 21 | | | | | 3 | | | 5 |
| 75 | | | | 41 | 15 | 16 | 26 | 12 | 33 | 21 | 17 | | | | | | | | | | | | | | | | | | | |
| 76 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 77 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | |
| 78 | 6 | | 3 | 4 | 4 | 2 | 1 | | 2 | | 1 | 1 | | | | | | | | | 7 | | | | 1 | 10 | 21 | 8 | 3 | 5 |
| 79 | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | |
| 80 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 81 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 82 | 1 | 2 | 16 | 25 | 32 | 6 | | 8 | 3 | 3 | 7 | 7 | | 2 | 1 | | 2 | | 2 | 3 | 36 | 35 | 29 | 30 | 1 | 17 | 58 | 6 | 4 | 6 |
| 83 | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | 1 | | | |
| 84 | | | | | | | | | | | 1 | | | | | | | | | | | | | | | 7 | 1 | | | |
| | 332 | 33 | 47 | 164 | 133 | 98 | 74 | 95 | 121 | 76 | 96 | 103 | 14 | 82 | 24 | 34 | 16 | 26 | 104 | 343 | 590 | 422 | 281 | 183 | 67 | 494 | 655 | 219 | 166 | 168 |

Table 2.—Continued.

| Taxon no. | 654 | 655 | 656 | 657 | 658 | 668 | 670 | 672 | 678 | 679 | 682 | 683 | 684 | 685 | 686 | 687 | 688 | 690 | 710 | 712 | 720 | 721 | 953 | 954 | 955 | 959 | 960 | 1357 | 1369 | 1370 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | | | | | | | 3 | 6 | 7 | 6 | 5 | 2 | 19 | | | | | 8 | | | | | | | | | 3 | | | |
| 2 | | | | | | | | | | | | | | | | | | | | | | | 1 | | 2 | | | | | |
| 3 | 9 | 15 | 17 | 2 | 38 | | | | | | | | | | | | | | 4 | | | | | 4 | 3 | 73 | 7 | | 1 | 2 |
| 4 | 1 | 2 | 1 | | | | | 2 | | | | | | | | | | | | | | | | | | 3 | 3 | | | |
| 5 | 1 | | | 5 | 1 | | 11 | 7 | 1 | | | | | 3 | 3 | | 3 | 1 | 92 | | 22 | 15 | | | | | 15 | | 1 | |
| 6 | | | | | | | | | | | | | | | | | | | | | | | | | | | 5 | 124 | | 3 |
| 7 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 8 | | | | | | | | 5 | 3 | 12 | 3 | 2 | 14 | 3 | 2 | 10 | 12 | 16 | | | 2 | | | | | | | | | |
| 9 | | | | | | | | | | | | 2 | | | | | | | | | | | | | | | | | | |
| 10 | | 14 | 4 | 73 | 20 | | | | | | | | | | | | | | 3 | | | | | 1 | 1 | 2 | 42 | | | |
| 11 | 2 | 1 | | | 5 | | | | | | | | | | | | | | | | | | | | 2 | 3 | | | | |
| 12 | | | | | | | 2 | 2 | | | | | | | | | | | | | | 3 | | | | | | | | |
| 13 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 14 | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | |
| 15 | | | | | 2 | 10 | 12 | 10 | 2 | 8 | 7 | 1 | 15 | | | 6 | | 3 | | | 8 | 5 | | | | | | | | |
| 16 | | | | | 3 | | | | | | | | | | | | | | | | | | | | | | 3 | | | |
| 17 | 3 | 2 | 5 | | 3 | | | | | | | | | | | | | | | | | | | | | 3 | | 3 | 3 | |
| 18 | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | 2 | | | |
| 19 | | | | | | 17 | 6 | 7 | 2 | | | | | | | | | | 12 | | 4 | 5 | | | | | 2 | | | |
| 20 | | | | | | 10 | | | 26 | 1 | 2 | | 1 | 3 | | | | | 6 | | 3 | 3 | | | | | 8 | 12 | | 119 |
| 21 | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | |
| 22 | 2 | 1 | | | 7 | | | | | | | | | 1 | 1 | | | 1 | | | | | | | | 2 | 4 | 2 | | 6 |
| 23 | | | | | 2 | 1 | | | | | | | 1 | 5 | 1 | | | | | | 2 | 5 | | | | | 3 | | | |
| 24 | | | | 5 | | | | | | | | | | | | | | | | | 1 | | | | | | 12 | | | |
| 25 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 26 | 2 | 4 | 16 | 2 | 10 | 1 | 27 | 27 | | 57 | 37 | 41 | 122 | 6 | 5 | 13 | 95 | 57 | 1 | 4 | | 1 | | 1 | | 32 | 14 | | | |
| 27 | 1 | | | 7 | | 2 | | 3 | 2 | | | 1 | | | 1 | | | | | | | | | 1 | | 1 | | | 1 | 2 |
| 28 | | 10 | 1 | 8 | 70 | | | 1 | | | | | | | | | | | 3 | | | 2 | 2 | 1 | 15 | | 32 | 9 | | |
| 29 | | 2 | 3 | 3 | 3 | 4 | 1 | 20 | 11 | 2 | 1 | | | 6 | | | 7 | 1 | | | 2 | 9 | | | | | | | | |
| 30 | | | | | 3 | 9 | 15 | 15 | 11 | 2 | | 1 | 3 | 10 | 5 | | 13 | | 21 | 11 | 16 | 5 | 2 | | | | 7 | 1 | 17 | |
| 31 | 4 | 3 | 7 | 7 | 6 | | | | | | | | | | | | | | | | | | | | | 4 | 2 | | | |
| 32 | 2 | | | | | | | | | | | | | | | | | | | | 2 | | | | | | 4 | | | |
| 33 | | | | | 1 | | | | | | | | | | | | | | 2 | | | | | | | | | 1 | | 26 |
| 34 | | 1 | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 35 | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | |
| 36 | 1 | 1 | | | | | | | | | | | | | | | | | 15 | | | | | | | | 1 | | | |
| 37 | | | | | | 2 | 30 | 6 | | 2 | | | | 9 | 2 | | 2 | 1 | | | 4 | 8 | | | | | | | 3 | |
| 38 | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 39 | | | | | | | | | | | | | | | 1 | | | | 8 | | | | | | | | | 151 | | 91 |
| 40 | | | | | 3 | 1 | | | 11 | 2 | 1 | 1 | | | | | 1 | 1 | 4 | | | | 2 | 1 | 1 | 1 | 3 | 18 | | |
| 41 | 7 | | 45 | 17 | 20 | | | | | | | | | | | | | | 1 | | | | 3 | 9 | 10 | 59 | 7 | 3 | | |
| 42 | 3 | | 2 | | | 2 | | | | | | | | 2 | 5 | | 12 | | | | 1 | | | | | | 4 | | | |
| 43 | 4 | 12 | 6 | 1 | 20 | 38 | 91 | 108 | 31 | 3 | 4 | 3 | | 33 | 32 | 1 | 31 | 2 | 4 | 4 | 67 | 48 | | | | 6 | 3 | 2 | 3 | 53 |
| 44 | | | 2 | | | | | | | | | | | 1 | | | 2 | | 13 | | 4 | | | | | | | | | |
| 45 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | |
| 46 | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 47 | | | | | 12 | | | | | | | | | | | | | | | | | | 21 | 32 | 23 | 25 | 6 | | | |
| 48 | | | 1 | | 1 | | 3 | 6 | | 1 | 4 | 2 | 1 | 1 | 2 | | 1 | 2 | | | 1 | 2 | | | | | | | | |
| 49 | | | | | | | | | | | | 1 | | | | | | | | | 2 | | | | | 1 | 2 | | | |
| 50 | | | 2 | | | | | | | | | | | | | | | | 4 | | | | | 2 | | 1 | | 2 | | |
| 51 | | | | | | | | | | | | | | | | | | | | | 5 | | | | | | | | | |
| 52 | | | | | | 14 | 9 | 23 | 4 | | 1 | 1 | | 3 | 2 | | 5 | | 4 | 2 | 7 | 9 | | | | | 3 | | | |
| 53 | | | 1 | 4 | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 54 | 2 | 4 | | | 3 | | | 3 | | | | | | | | | | | 1 | | | 1 | | 2 | 2 | 2 | | | | |
| 55 | | 2 | 3 | 1 | 13 | 12 | 1 | 2 | 13 | 2 | | 2 | | 16 | 5 | | 16 | | 6 | | 26 | 27 | 1 | | 1 | 8 | 9 | 6 | 1 | 200 |
| 56 | | | | | | | | 3 | | | | | | | | | | | | | | | | | | | | | | |
| 57 | 5 | 4 | 3 | | 5 | | | | | | | | | | | | | | | | | | | | | 3 | | | | |
| 58 | 2 | | 11 | 1 | 6 | | | | | | | | | | | | | | | | | | | | | | | 4 | 4 | |
| 59 | | | | | | 12 | 63 | 34 | 14 | 6 | 5 | 7 | 2 | 12 | 7 | 9 | 44 | 8 | | 1 | 7 | 3 | | | | | 4 | | 23 | |
| 60 | | | | | | | | | 10 | 1 | | | | | 2 | | 2 | | | 1 | | | | | | | | | 5 | 39 |
| 61 | | 7 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | |
| 62 | 3 | | | | | | | | | | | | | | | | | | | | | | | | | 2 | | | | |
| 63 | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | |
| 64 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 65 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 66 | | | | | | 1 | | | 2 | 5 | 3 | | 4 | | | | 16 | 4 | 2 | | | | 17 | 36 | 87 | 29 | | | | 4 |
| 67 | | 4 | 1 | | 4 | | | | | | | | | | | | 3 | | | | | | | | 1 | 2 | | 1 | | |
| 68 | | | | | | 1 | | 4 | 1 | 1 | | | | | 3 | | | | | | | | | | | | | | | |
| 69 | | 1 | | | | | | | 19 | | | | | | 24 | 2 | | | 22 | 28 | | | | | 1 | | | | 19 | 2 |
| 70 | | | | | | | | | | | | | | | | | | | | 123 | | | | | | | | | 288 | |
| 71 | 2 | | | | | | | | | | | | | | | | | | 1 | | 2 | | | | | | 7 | | | 54 |
| 72 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 73 | 3 | 9 | 3 | 5 | 12 | 7 | | | 11 | | | 4 | 3 | | | | | | | | | 4 | 1 | | | 6 | 13 | 136 | | 20 |
| 74 | | | | | 2 | 188 | 19 | 37 | 44 | 12 | 5 | | | 14 | 8 | | 32 | 7 | 56 | | | | | | | | 60 | 4 | | |
| 75 | | | | | | | | | | | | | | | | | | | | | 87 | 76 | | | | | | | | |
| 76 | | | | | | | | | | | | | | | | | | | | | 27 | | | | | | | | | |
| 77 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 78 | 1 | 5 | 2 | 1 | 6 | 1 | 3 | 2 | | 9 | 8 | 3 | 1 | 3 | 2 | | 27 | | 1 | | | | | | | | | 1 | | |
| 79 | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | |
| 80 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 81 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 4 |
| 82 | 1 | 4 | 2 | 1 | 63 | 7 | 16 | 1 | 9 | 12 | 4 | 8 | 11 | 1 | | | 29 | 9 | 71 | | 3 | 3 | 1 | | | 26 | 7 | 82 | 3 | 36 |
| 83 | 3 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 84 | | | | 1 | | | | | | | | | | | | | | | | | 2 | | | | | | | | | 1 |
| | 65 | 111 | 138 | 145 | 344 | 340 | 312 | 335 | 234 | 144 | 90 | 82 | 198 | 132 | 113 | 41 | 353 | 121 | 357 | 175 | 307 | 236 | 51 | 90 | 149 | 295 | 297 | 563 | 373 | 662 |

Table 2.—Continued.

| Taxon no. | 1371 | 1375 | 1376 | 1392 | 1393 | 1394 | 1395 | 1396 | 1397 | 1398 | 1399 | 1400 | 1401 | 1402 | 1403 | 1404 | 1405 | 1406 | 1433 | 1434 | 1435 | 1436 | 1438 | 1442 | 1480 | 1481 | 1482 | 1483 | 2003 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 20 | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 2 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 3 | 1 | 15 | 25 | | | | | | | | | | | | | | | | 10 | 2 | | | | | 20 | | 22 | 2 | |
| 4 | 3 | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 5 | 2 | 1 | 2 | | | | 3 | | | | | | | 9 | 30 | 24 | 32 | 5 | | 2 | | | 12 | | 2 | 34 | 175 | 82 | 2 |
| 6 | | 34 | | | 2 | | | | | | 5 | | 7 | 4 | 22 | | | | 43 | | | 1 | 32 | 17 | | | 91 | | 4 |
| 7 | 18 | | | | | | | | | | | | | | | | | | | | | | | | | | | | 2 |
| 8 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 9 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 10 | | 7 | | | | | | | | | | | | | | | | | 4 | | | | | | 3 | 1 | | 3 | |
| 11 | | | | | | | | | | | | | | | | | | | | | | | | | 4 | | | | |
| 12 | | 1 | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | |
| 13 | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | 4 | | |
| 14 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 15 | 16 | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 16 | 11 | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | 5 | |
| 17 | 4 | 5 | | | | | | | | | | | | | | | | | | | | | | | | | 3 | 2 | |
| 18 | | | | | | | | | | | | | | | | | | | | | 2 | | | | | | | | |
| 19 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 20 | | 22 | | 67 | 51 | 29 | 41 | 14 | 16 | 11 | 18 | | 23 | | | | | | 3 | | 2 | | 2 | | | | 4 | | |
| 21 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 22 | 1 | 3 | | 3 | 2 | 2 | 1 | 2 | 1 | 4 | 2 | | 1 | | | | | | | | 2 | | | | | | | | |
| 23 | | | | | | | | | | | | | | | | | | | | | | | 3 | | | | | | |
| 24 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 25 | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | |
| 26 | 9 | 8 | 1 | | | | | | | | | | | | | | | | | | | | | | 10 | 6 | 7 | 8 | 4 |
| 27 | | 1 | | 2 | | | | | | | 3 | | 7 | | | | | | | | 3 | 2 | 5 | 2 | | 1 | 2 | 10 | 2 |
| 28 | 6 | 89 | 3 | | | | | | | | | | 1 | | | | | | 6 | | | | 7 | | 13 | 5 | 10 | 3 | |
| 29 | | 5 | | | | | | | | | | | | | | | | | 3 | | | | | | 2 | 2 | | | |
| 30 | 6 | 16 | 1 | | | | | | | | | | 4 | | | | | | | | 2 | | 3 | 1 | 1 | | 11 | 10 | |
| 31 | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | |
| 32 | | 2 | | | | | | | | | | | | | | | | | | | | | | | | 2 | | 2 | |
| 33 | | | 1 | 18 | 10 | 10 | 12 | 5 | 4 | 15 | 10 | | 17 | | | | | | 44 | | | | 1 | | | | 20 | | |
| 34 | | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 35 | | | | | | | | | | | | | | | | | | | | | | | | 2 | | | | | |
| 36 | | | | | | | | | | | | | | | | | | | 9 | | | | | | | | 13 | | |
| 37 | | | | | | | | | | | | | | | | | | | | | | | | | 1 | 4 | | 1 | |
| 38 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 39 | | 21 | 2 | 48 | 21 | 57 | 206 | 157 | 16 | 51 | 36 | 4 | 114 | | | | | | 4 | | | 1 | | 3 | | | 11 | | |
| 40 | | 11 | | | | | | | | | | | | | | | | | 6 | | | | 3 | | | | 4 | 2 | |
| 41 | | 32 | 48 | | | | | | | | | | | | | | | | 4 | | | | | | 81 | 3 | | 11 | |
| 42 | 16 | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | |
| 43 | | 13 | 4 | 177 | 49 | 37 | 95 | 92 | 22 | 31 | 81 | 6 | 290 | | | | | 2 | 5 | | 16 | | | 44 | | | 133 | 4 | 2 |
| 44 | 11 | | | | | | | | | | | | | | | | | | 13 | 1 | | | 2 | 2 | | 3 | 41 | 13 | |
| 45 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 46 | | | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 47 | | 15 | 1 | | | | | | | | | | | | | | | | | | | | | | 28 | 2 | | 4 | |
| 48 | | | | | | | | | | | | | | | | | | | | | | | | | | | 2 | 21 | |
| 49 | | | | | | | | | | | | | | | | | | 4 | | | | | | | | 2 | 1 | | |
| 50 | | 2 | 2 | | | | | | | | | | | | | | | | 2 | | | | | | | | 12 | | |
| 51 | 1 | | | | | | 3 | | | | | | | | | | | | | | | | | | | | 5 | | |
| 52 | | 12 | | 6 | 3 | 6 | 4 | 8 | 1 | 3 | 1 | 3 | 43 | | | | | | | | | | | | 1 | 2 | | 4 | |
| 53 | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | |
| 54 | 4 | | | | | | | | | | | | | | | | | | | | | | | | 2 | 1 | | | |
| 55 | 2 | 11 | 1 | 121 | 98 | 75 | 98 | 62 | 53 | 81 | 72 | 8 | 444 | | | | | 43 | 6 | | 4 | | 13 | 7 | 1 | 1 | 35 | 4 | |
| 56 | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | 2 | 1 | |
| 57 | | | 2 | | | | | | | | | | | | | | | | | | | | | | | | 7 | | |
| 58 | | | | | | | | | | | | | | | | | | | | | | | | | | | | 4 | |
| 59 | 157 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 6 | | |
| 60 | 4 | | | 13 | 10 | 14 | 9 | 7 | 6 | 7 | 18 | | 21 | | | | | | | | | | | | | | 1 | | |
| 61 | | | | | | | | | | | | | | | | | | | | | | | | | 4 | | | | |
| 62 | | | | | | | | | | | 17 | | | | | | | | | | | | | | | | 10 | | |
| 63 | 38 | | | | | | | | | | | | | | | | | | 8 | | 7 | | 4 | | | | 15 | | 6 |
| 64 | | 1 | | | | | | | | | | | | | | | | | 4 | | | | 3 | | | | 2 | 1 | |
| 65 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 66 | 80 | | | 12 | | | 4 | 8 | | | 2 | | | | | | | | | | | | | | 61 | 1 | | | |
| 67 | 39 | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | |
| 68 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 69 | 14 | 9 | | | | 2 | | 6 | | | | | | | | | | | | | | | | | | | 1 | | |
| 70 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 71 | | | | 42 | 16 | 2 | 47 | 5 | 4 | | 43 | | 3 | | | | | | | | | | | 4 | | | | | |
| 72 | | | | | | | | 1 | | 4 | 1 | 3 | 43 | | | | | | | | | | | | | | | | |
| 73 | 2 | 5 | 1 | 334 | 68 | 73 | 144 | 68 | 29 | 33 | 33 | 16 | 365 | | 2 | | | 1 | 14 | 1 | 11 | 3 | 2 | 45 | 4 | 9 | 68 | 4 | 1 |
| 74 | | 168 | | | | | | | | | | | | | | | | | | | | | | | | 4 | 6 | 26 | |
| 75 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 76 | | | | | | | 77 | | | | | | | | | | | | | | | | | | | | | | |
| 77 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 78 | 11 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 79 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 80 | | | | | | | | | | | | | | | | | | | | | | | | | | | 7 | | |
| 81 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 82 | 33 | 11 | 3 | 46 | 3 | 6 | 1 | 6 | 27 | 3 | 64 | 6 | 117 | | 14 | | | | 24 | 2 | 2 | | 5 | 18 | | | 160 | 8 | 1 |
| 83 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 84 | | 1 | 3 | | | | | | | | | | | | | | | | | | | | 5 | | | 1 | 2 | 2 | |
| | 509 | 527 | 102 | 889 | 333 | 313 | 745 | 441 | 179 | 243 | 406 | 46 | 1501 | 13 | 68 | 24 | 32 | 55 | 215 | 8 | 51 | 7 | 102 | 145 | 238 | 86 | 894 | 239 | 24 |

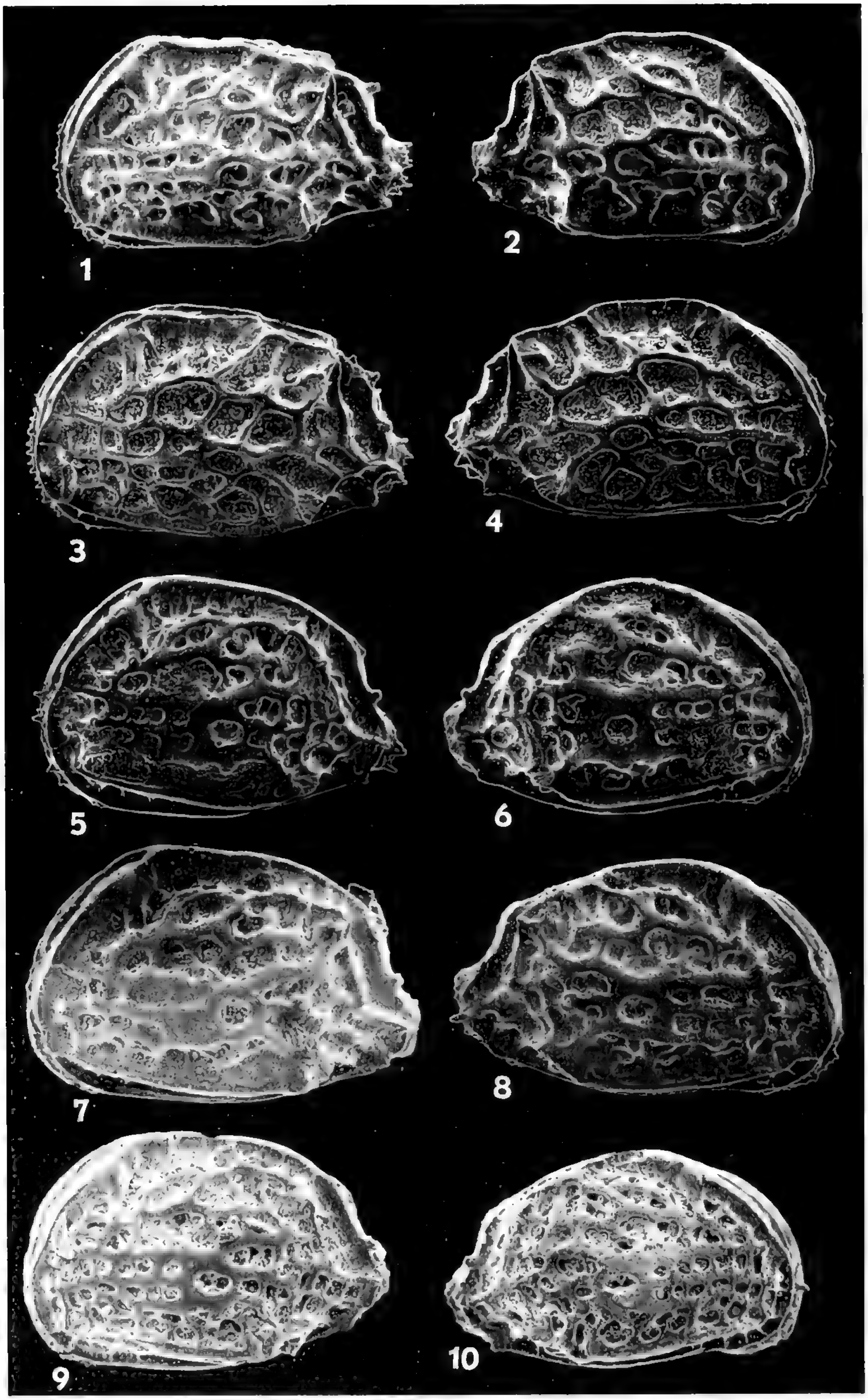

PLATE 1

1–2. *Radimella confragosa* (Edwards, 1944), ×118.
  1. LV, F, Locality PPP 678, Rio Banano Formation, USNM 490889.
  2. RV, F, Locality PPP 369, Escudo de Veraguas Formation, USNM 490890.

3–4. *Radimella wantlandi* Teeter, 1975, ×118.
  3. LV, F, Locality PPP 638, Moin Formation, USNM 490891.
  4. RV, F, Locality PPP 638, Moin Formation, USNM 490892.

water deeper than 2000 m, and as fossil, 50–90% of North Atlantic Ocean Pliocene assemblages (Rodriguez-Lazaro and Cronin, in press). Species of *Krithe* rarely inhabit shallow-water environments; the best known shallow-water species is *K. praetexta* (Sars, 1866), which lives in shelf and slope areas off northern Europe (Athersuch *et al.,* 1989). A few sighted *Krithe* also live in shallow-water around Australia (Whatley *et al.,* 1983). In the Gulf of Mexico and Caribbean Sea, *Krithe* is also usually found on the continental slope and deeper waters (Morkhoven, 1972), with the important exception of the Paria-Trinidad-Orinoco Shelf (see below and Fithian, 1980, App. 1). Most species of *Bradleya* are also most common in deep-sea environments (Benson, 1972; Whatley *et al.,* 1983), with the exceptions of *B. normani* (Brady, 1866), which inhabits continental slopes and fjords of southern South American (Shuckstes, 1995; Whatley *et al.,* in press), and *B. andamanae* Benson, 1972, which lives in depths of 70–500 m in the northeastern Indian Ocean (Benson, 1972).

The database of modern ostracodes from the Caribbean and Gulf of Mexico allows us to identify modern environments in which the mixture of species found in Biofacies A occurs today. The only place identified in the Caribbean where *Krithe* and *Bradleya* occur together with shallow-water taxa is the Paria-Trinidad-Orinoco Shelf off northern Venezuela (Fithian, 1980; Bold, 1978a), a region of modern tropical coastal upwelling water.

A similar anomalous shallow-water colonization of *Krithe* and *Bradleya* occurs in the southern part of the Magellan Straits, where these and other normally psychrospheric, blind taxa occur together with the indigenous shallow-water assemblage (Whatley *et al.,* in press). Whatley *et al.* (in press) interpreted the occurrence of these taxa in shallow-water as due to cold water temperatures and upwelling.

A relatively shallow paleodepth for the Cangrejos Creek and lower part of the Lomas del Mar localities of the Moin Formation is suggested by the strong development of the eye tubercle in *Echinocythereis madremastrae* (Pl. 3, Fig. 2). It is well known that ostracodes living in deep water below the euphotic zone (< about 100–200 m) do not develop prominent eye tubercles as do most of those living in shallow-water (Benson, 1975; Howe and Bold, 1975). Moreover, Kontrovitz and Myers (1988) quantified the relationship between ostracode ocular structures and ambient downwelling sunlight in seawater and concluded that the biconvex eyespot-tapetum structure typical of podocopid ostracodes like *Echinocythereis* would be of no use below depths of about 280 m in clear ocean water and 85 m in more turbid coastal water.

The combination of ecological data for colder water conditions and morphological evidence for shallow-water paleoenvironments (<100–200 m), leads us to postulate that Biofacies A represents an outer shelf to upper slope environment, perhaps similar to that off northern Venezuela where *Krithe* and *Bradleya* live today. The upwelling of cool, nutrient-rich water that characterizes the Venezuela shelf, and elsewhere, appear to be the typical oceanographic conditions that allow *Krithe* and *Bradleya* to migrate upslope into relatively shallow-water habitats.

Benthic foraminiferal assemblages from the type Moin section support the interpretation of a depositional environment at the continental shelf edge (150–250 m of water depth), as they include a mixture of shelf edge and nearshore taxa (Cassell, 1986; Collins *et al.,* 1995a). Collins *et al.* (1995a) interpreted the foraminiferal assemblages as evidence for downslope transport of nearshore taxa; Collins *et al.* (1995b) suggested benthic foraminifera assemblages were not representative of upwelling assemblages. Nonetheless, oceanographic parameters such as dissolved oxygen, nutrients, food, temperature, light, rather than simply abstract water depth, are the critical factors that influence ostracode species' ecology and their depth distributions. For example, oceanographic factors have been shown to be especially important for deep-sea and mid-depth taxa living along the continental slope, where bottom water temperatures in the thermocline limit the shallowest depth for many species (Dingle and Lord, 1990; Dingle *et al.,* 1989; Rodriguez-Lazaro and Cronin, in press). Off southwest Africa (south of

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5–6. *Radimella ovata* Bold, 1988, ×118
    5. LV, F, Locality PPP 68, Isla Solarte, USNM 490893.
    6. RV, F, Locality PPP 68, Isla Solarte, USNM 490894.
7–8. *Radimella* aff. *R. ovata* Bold, 1988, ×118.
    7. LV, F, Locality PPP 631, Moin Formation, USNM 490895.
    8. RV, F, Locality PPP 631, Moin Formation, USNM 490896.
9–10. *Radimella ovata* Bold, 1988 ×109.
    9. LV, F, Locality PPP 678, Rio Banano Formation, USNM 490897.
    10. RV, F, Locality PPP 678, Rio Banano Formation, USNM 490898.

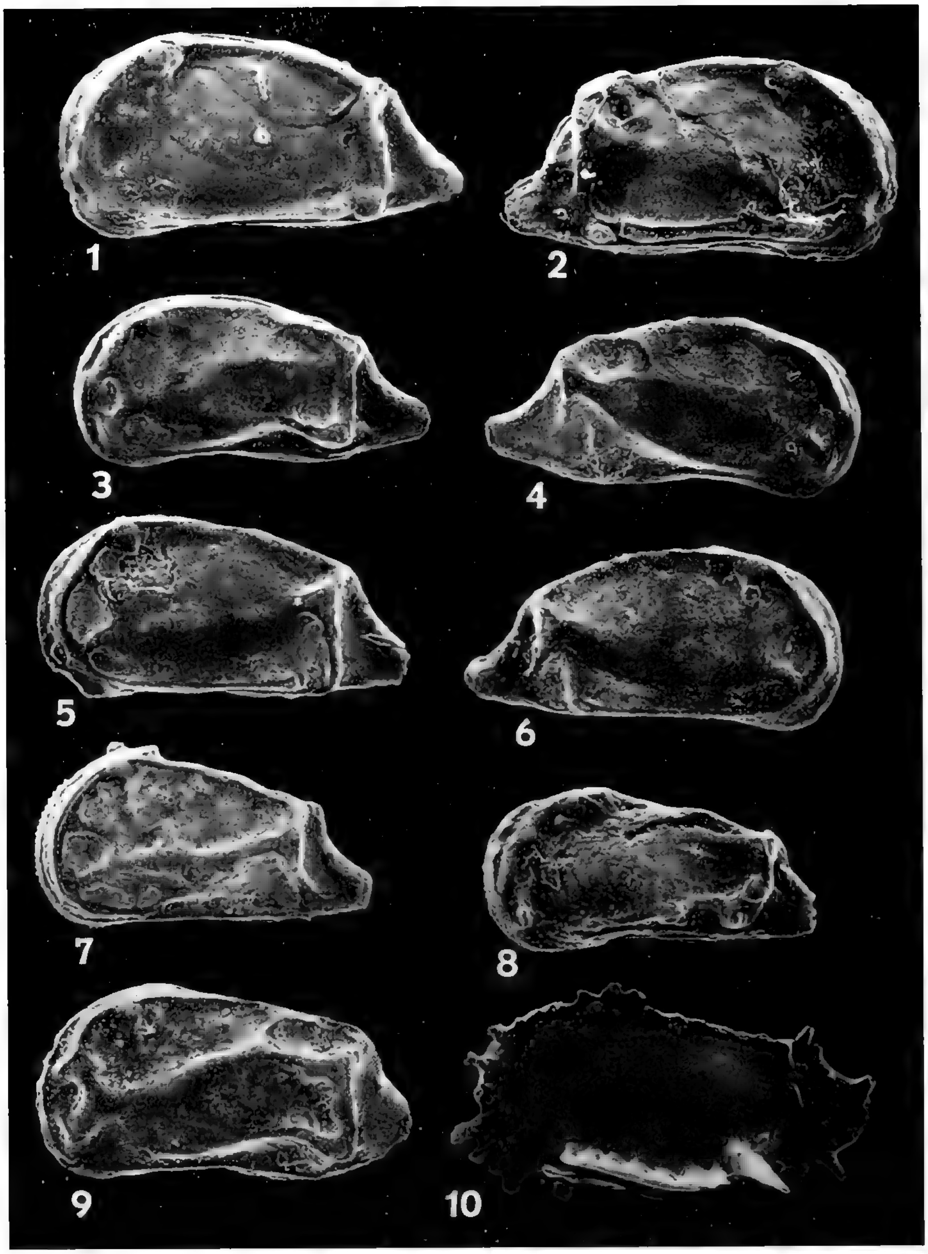
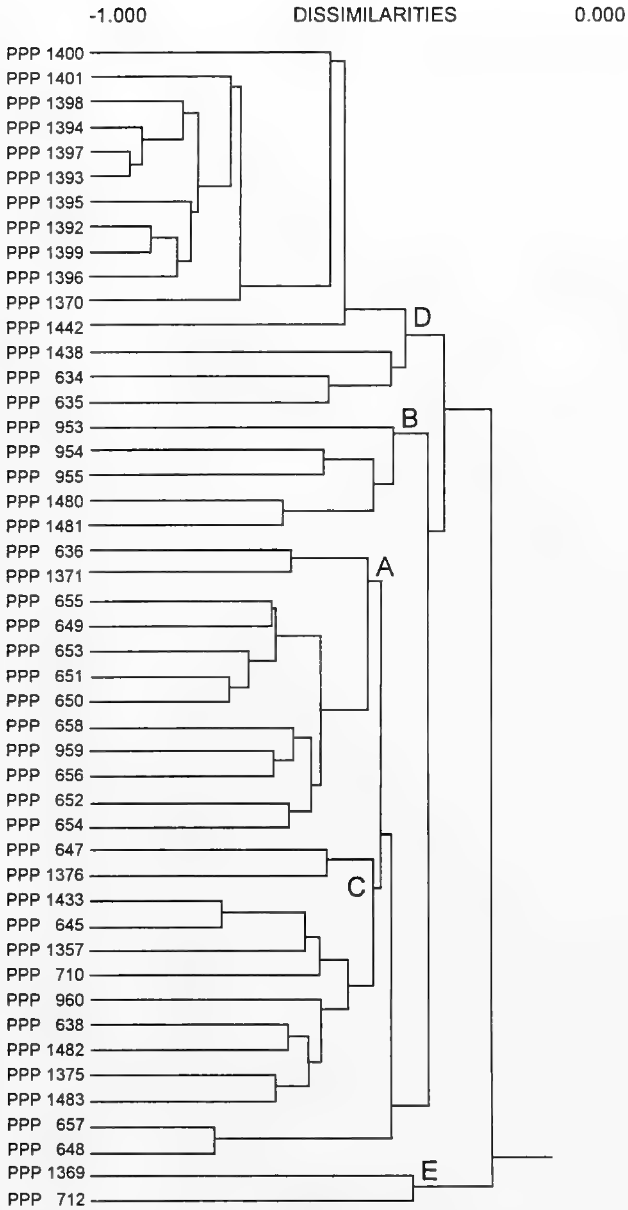


PLATE 2

1–2. *Caudites medialis* Coryell and Fields, 1937, ×120.
  1. LV, Locality PPP 668, Rio Banano Formation, USNM 490899.
  2. RV Locality PPP 668, Rio Banano Formation, USNM 490900.
3–4. *Caudites* aff. *C. rectangularis* (Brady, 1869), ×120.
  3. LV, Locality PPP 606, Rio Bartolo, USNM 490901.
  4. RV, Locality PPP 768, Rio Banano Formation, USNM 490902.
5–6. *Caudites* cf. *C. asymmetricus* Bate *et al.*, 1980, ×120.
  5. LV, Locality PPP 63, Cayo Agua, USNM 490903.
  6. RV, Locality PPP 63, Cayo Agua, USNM 490904.
7. *Caudites medialis* Coryell and Fields, 1937, ×120.
  LV, Locality PPP 62, Cayo Agua Formation, USNM 490905.
8. *Caudites nipeensis* Bold, 1946, ×120.
  LV, Locality PPP 369, Escudo de Veraguas Formation, USNM 490906.
9. *Caudites rectangularis* (Brady, 1869), ×120.
  LV, Locality PPP 655, Moin Formation, USNM 490907.
10. *Pterygocythereis* sp., ×94.
  LV, Locality PPP 653, Moin Formation, USNM 490908.



Text-figure 1.—Q-mode dendrogram of cluster analysis, average linkage method, of Jaccard coefficients, based on 57 localities from the Moin and Rio Banano formations, Limon Basin, Costa Rica. Letters A–E refer to ostracode biofacies that are characteristic of faunal assemblages and indicative of distinct environments of deposition. See text for further explanation.

28°S), Dingle (1992a, 1992b) found that shelf upwelling and intrusion of shelf currents, especially the cold, low-salinity, nutrient-rich Antarctic Intermediate Water, controls the distribution of ostracode species. Whatley (1991) also demonstrated the influence of low oxygen in slope environments for certain platycopid ostracodes. In summary, we favor an "oceanographic" interpretation of the depositional environment for Biofacies A of the Moin Formation—that the ostracodes indicate cool water (12–15° C) on the outer shelf/upper slope, perhaps due to upwelling of cold, deep nutrient-rich waters.

### *Biofacies B*

Biofacies B is represented by Cluster B (Text-fig. 1) and is composed of five samples from the Lomas del Mar locality containing assemblages that are similar to those of Biofacies A in that they also contain significant numbers of *Krithe* spp. (7%), although in smaller numbers than for Biofacies A. Biofacies B is also distinguished from Biofacies A by higher proportions of neritic ostracodes, including *Pseudosammocythere* sp. (average 32%), *Munseyella bermudezi* Bold, 1966 (21%), *Radimella confragosa* (5%) and *Cytherella* spp. (4%). The *in situ* coral lenses from which the microfossil samples were collected indicate a water depth of less than 40 m (A. F. Budd, 1996, written communication). If the interpretation of the depositional environment for Biofacies A is correct, then the presence of *Krithe* and other normally deeper-dwelling ostracodes in the Lomas del Mar reef sediments suggest upwelling of cooler waters occurred during the deposition of this unit.

### *Biofacies C*

Biofacies C is represented by samples from Cluster C (Text-fig. 1) and consists of 13 samples that are primarily from Lomas del Mar and Avenida Barracuda outcrops. Biofacies C appears to be transitional between the cooler upwelling assemblages of Biofacies A and the shallow (<30 m) carbonate platform assemblages of Biofacies D (see below). The dominant taxa that clearly indicate a relatively shallow, primarily warm-water, tropical environment are the bairdiids (16%; *i.e., Bairdoppilata, Neonesidea, Paranesidea*), *Xestoleberis* spp. (10%), *Jugosocythereis pannosa* (Brady 1869) (5%), *Loxocorniculum* spp. (8%) and *Radimella confragosa* (11%). If the interpretation of the occurrence of typical deep-water taxa *Krithe* and *Bradleya* (14% and 9%, respectively, in this biofacies) presented above is correct, then there was at least periodic upwelling of cooler deep-water during the deposition of Biofacies C, although there may be more time-averaging than occurred in Biofacies A.

### *Biofacies D*

Cluster D (Text-fig. 1) consists of 15 samples, most of which are from a single outcrop (CTA Fence locality, Rio Banano Formation), and represents Biofacies D. Four taxa dominate this assemblage: *Radimella confragosa* (18%), *Loxocorniculum* spp. (16%), *Paracytheridea tschoppi* Bold, 1946 (20%), and *Jugosocythereis pannosa* (14%). Other important occurrences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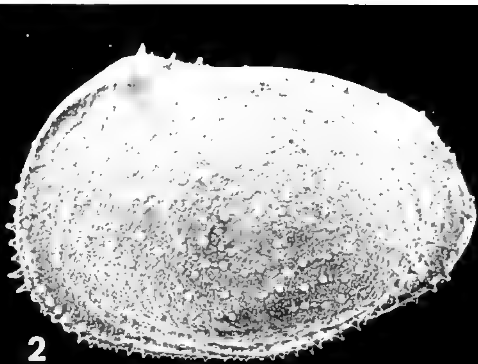
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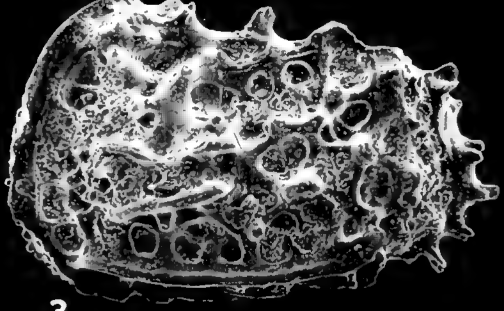
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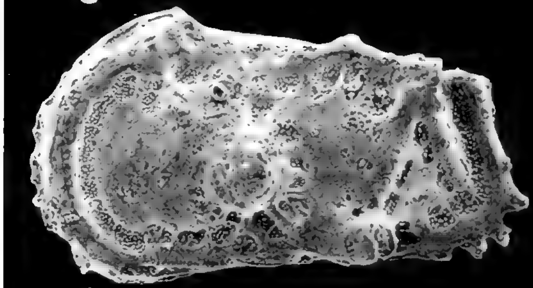
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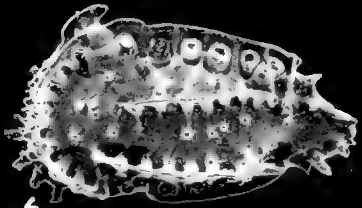
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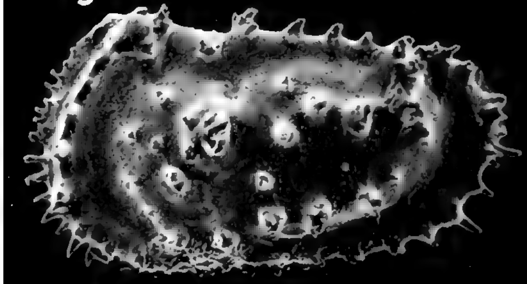
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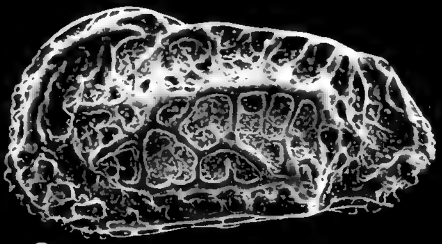
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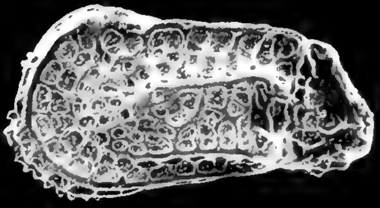
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PLATE 3

1. *Bradleya* aff. *B. acceptabilis* Lübimova and Sánchez-Arango, 1974, ×99.
   LV, F. Locality PPP 657, Moin Formation, USNM 490909.
2. *Echinocythereis madremastrae* Bold, 1988, ×90.
   LV, F. Locality PPP 653, Moin Formation, USNM 490910.

include *Caudites nipeensis* Bold, 1946, *Orionina vaughani* (Ulrich and Bassler, 1904), *Gangamocytheridea? plicata* Bold, 1968, *Quadracythere howei* (Puri 1953), and *Perissocytheridea subrugosa* (Brady, 1870). This assemblage is found in the lower part of the CTA Fence section and signifies a shallow-water carbonate assemblage (water depth <10 m; Teeter, 1975) distinct from assemblages in Biofacies A–C.

### *Biofacies E*

Only two samples cluster in this group (Cluster E) and represent Biofacies E (Text-fig. 1). They are dominated by *Reussicythere reussi* Teeter, 1975, described from the nearshore areas and main lagoon of Belize. This species accounts for an average of 74% of the total valve count in each sample. Also present are *Puriana* aff. *P. matthewsi* Teeter, 1975, (11% average between the two samples), *Cytherura* sp. (5%) and *Pellucistoma howei* Coryell and Fields, 1937 (3%). The low diversity and the high dominance of only a few taxa suggest that this biofacies represents an assemblage living in an environmentally restricted nearshore environment.

### *Spacial and Temporal Relationships of Limon Area Samples*

The biofacies of the Moin Formation described above reflect spatially and/or temporally complex environments of deposition. Analysis of these fossil ostracode assemblages has provided insight as to the potential stratigraphic relationships among several stratigraphic sections of the Moin Formation and a more detailed understanding of the late Pliocene and early Pleistocene environmental history in the Limon Basin. If we assume the *Bradleya*- and *Krithe*-bearing finer-grained sediments (Biofacies A and B) stratigraphically underlie the reef facies (Biofacies C) at the Lomas del Mar site (Text-fig. 3a), our results indicate a deep to shallow environmental change in the Moin Formation and/or a diminished upwelling towards the upper part of the section. An alternative interpretation (McNeill, written communication, 1995) is that the upwelling assemblages (Biofacies A) represent a transgression that postdates the deposition of the reef facies at the Lomas del Mar site. Such a scenario implies that these sediments were draped along the flanks of the Lomas del Mar reef and also in the low-lying Cangrejos creek area (Text-fig. 3b). Given the absence of core data for this geographic area, clarification of the stratigraphic relationships for this portion of the Moin Formation will depend on additional geologic mapping and refinement of the ages based on biostratigraphic and magnetostratigraphic work.

The distinct clustering (Biofacies D) of many CTA Fence samples suggests that this section represents a reefal facies different from, and probably older than that at Lomas del Mar, an interpretation that is consistent with the field relationships of the two sections (Coates, this volume; Budd *et al.,* this volume). Previous geologic mapping has assigned the CTA Fence and Quebrada Chocolate sections to the Rio Banano Formation (Taylor, 1975; Cassell and Sen Gupta, 1989; Coates *et al.*, 1992). McNeill *et al.* (in press) have now described the Quebrada Chocolate Formation, which includes these older trend outcrops. The Quebrada Chocolate section is located 2 km west of the CTA Fence section and contains ostracodes typical of the older Rio Banano Formation samples (*Basslerites* spp., *Perissocytheridea* spp., *Puriana* spp.), supporting the hypothesis that the Quebrada Chocolate section is part of a reefal trend older than the Lomas del Mar trend. Although this reefal unit has a similar carbonate platform ostracode assemblage to that of the Lomas del Mar reefal facies, it is distinguished from the younger

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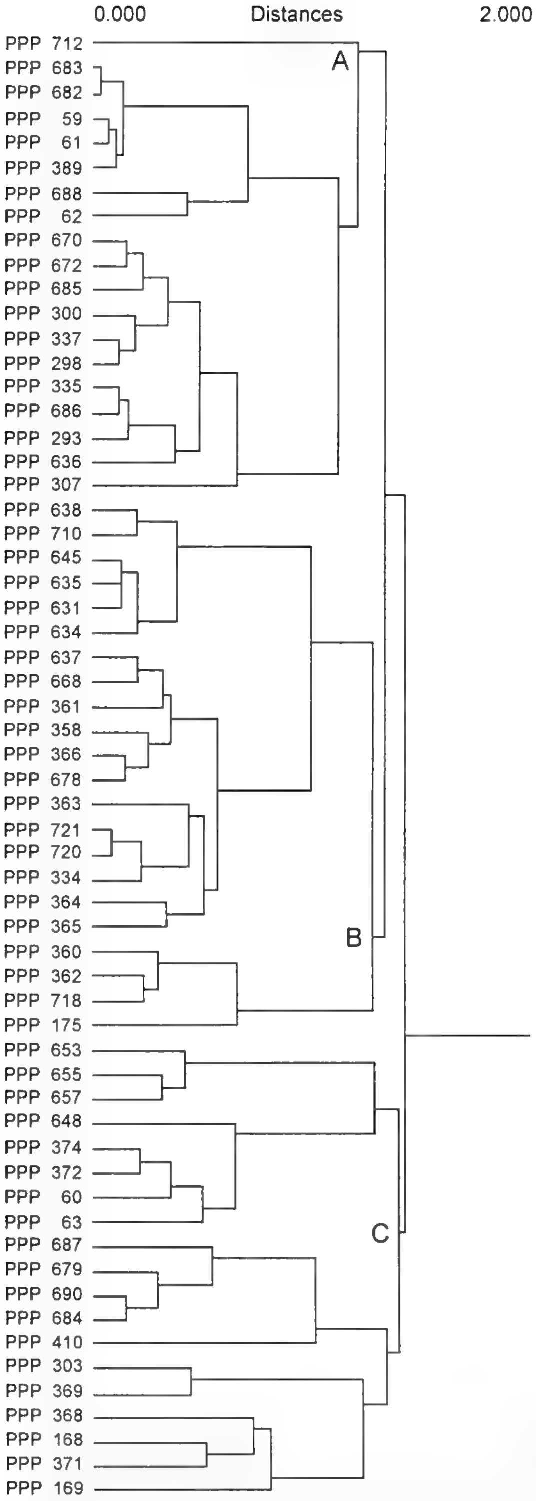
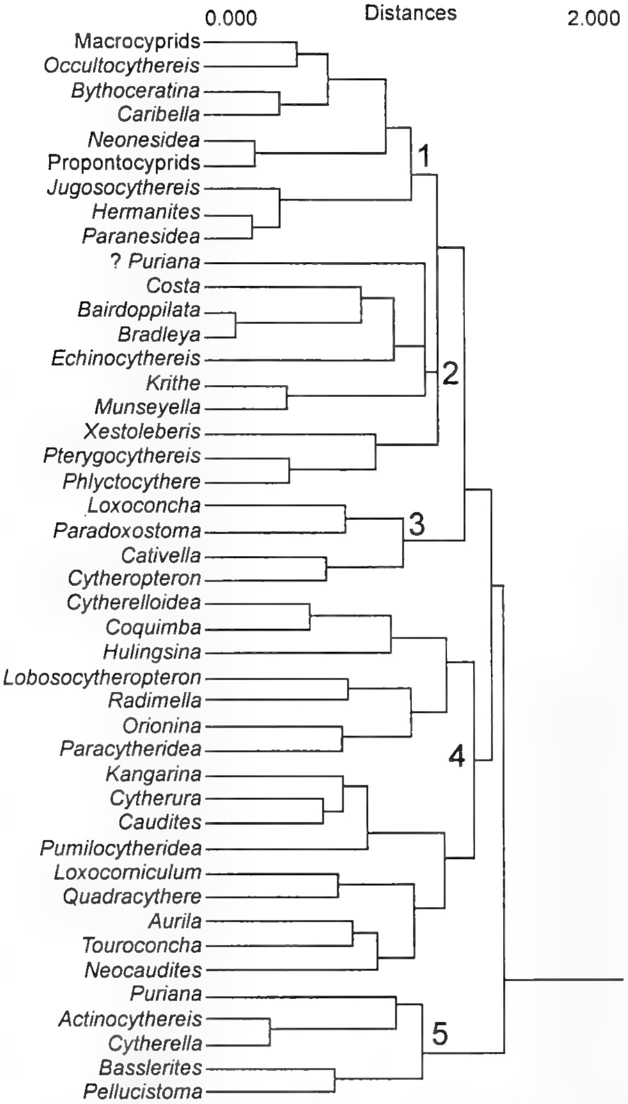
3. *Jugosocythereis pannosa* (Brady, 1869), ×108.
   LV, F, Locality PPP 710, Moin Formation, USNM 490911.
4. *Quadracythere howei* (Puri, 1953), ×162.
   LV, F, Locality PPP 710, Moin Formation, USNM 490912.
5. *Hermanites hornibrooki* Puri, 1960, ×162.
   LV, F, Locality PPP 710, Moin Formation, USNM 490913.
6. *Cativella navis* Coryell and Fields, 1937, ×108.
   LV, F, Locality PPP 682, Rio Banano Formation, USNM 490914.
7. *Actinocythereis gomillionensis* (Howe and Ellis, 1935), ×108.
   LV, F, Locality PPP 673, Rio Banano Formation, USNM 490915.
8. *Costa* aff. *C. bellipulex* Levinson *in* LeRoy and Levinson, 1974, ×108.
   LF, F, Locality PPP 368, Escudo de Veraguas Formation, USNM 490916.
9. *Costa variabilicostata recticostata* Bold, 1970, ×108.
   LV, F, Locality PPP 631, Moin Formation, USNM 490917.
10. *Krithe* sp.
   RV, F, internal view, ×135, Locality PPP 657, Moin Formation, USNM 490918.



Text-figure 2a.—Q-mode dendrogram of cluster analysis of Jaccard coefficients, complete linkage method, showing relationship of Limon Basin, Costa Rica, and Bocas del Toro Basin, Panama, ostracode assemblages. A. Samples primarily from Rio Banano and Caya Agua formations. B. Samples from Moin and Escudo de Veraguas formations. C. Samples from Caya Agua, Valiente Peninsula, Escudo de Veraguas (southern coast), Moin and Rio Banano formations.

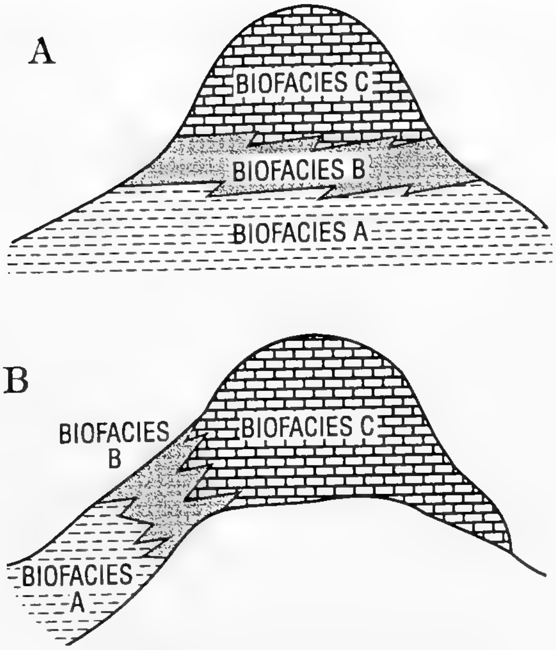


Text-figure 2b.—R-mode dendrogram showing relationship of taxa from the same cluster analysis as Text-figure 2a: 1, 4. Taxa representative of carbonate lagoon environments. 2. Outer shelf to upper slope taxa. 3. Taxa representative of lagoon environments, some of which prefer phytal habitats. 5. Taxa that prefer fine-grained, muddy substrates.

Lomas del Mar reefal facies by its lack of deeper-water ostracodes. Efforts are underway to revise the geologic map of the geologically complex Limon area and to elucidate the stratigraphic relationships between the reef exposures and intervening clastic deposits (McNeill *et al.,* 1996; McNeill *et al.,* in press).

## Rio Banano Formation

Assemblages from exposures of the Rio Banano Formation south of the city of Limon contain a very distinct assemblage containing *Basslerites* spp., *Cytherella* spp., *Cativella navis* Coryell and Fields, 1937,



Text-figure 3.—Spatial and temporal relationship of selected samples from Biofacies A–C (Text-fig. 1) in the Limon area.
3a. Relationship of ostracode Biofacies A–C as proposed herein. Biofacies A = deeper water ostracode assemblage (possibly upwelling related). Biofacies B = transitional assemblage of deeper water ostracodes and shallower carbonate-platform ostracodes. Biofacies C = carbonate-platform ostracode assemblage with fewer deeper-water ostracodes. The grain-size generally coarsens upward from predominantly claystone in Biofacies A (with some intervals of coarser material) to a silty sandstone in Biofacies C.
3b. Alternative interpretation of relationship of ostracode Biofacies A–C (McNeill, written communication, 1995). Biofacies A postdates or is coeval to Biofacies B and C. Finer-grained sediments have been draped along flanks of Lomas del Mar reef trend.

*Loxocorniculum* spp., *Pellucistoma howei, Puriana* spp., and *Radimella ovata* Bold, 1988. The presence of *Actinocythereis gomillionensis* (Howe and Ellis, 1935) is noteworthy because it is not found in other formations in the Limon area (with the exception of two samples of the Moin Formation) nor in the Bocas del Toro area. The Rio Banano Formation ostracode assemblages are lacking in typical carbonate platform taxa (*e.g., Jugosocythereis, Hermanites, Radimella wantlandi* Teeter, 1975, *Quadracythere* spp.). The environment of deposition was probably inner to middle continental shelf, near a delta or estuary that was providing clastic sediment. This interpretation is corroborated by the benthic foraminiferal assemblages of the Rio Banano Formation, which indicate deposition in 10–40 m of water in an open marine, inner to middle neritic environment (Cassell, 1986; Cassell and Sen Gupta, 1989; Collins *et al.*, 1995), with a slight deepening higher in the section (Cassell, 1986; Cassell and Sen Gupta, 1989). It is possible that there were periods of non-marine deposition and/or depositional hiatuses within the Rio Banano section in areas lacking good exposures.

## OSTRACODES FROM BOCAS DEL TORO BASIN, PANAMA

At present, ostracodes have been studied from only a few samples from the Nancy Point Formation (Appendix A, Map 5) and they contained an outer shelf to upper slope assemblage including the following genera *Argilloecia, Ambocythere, Cytherella, Krithe,* and *Munseyella.* Cayo Agua Formation (App. A, Map 6) ostracode assemblages generally contain typical shallow marine, tropical taxa such as *Cativella navis, Loxocorniculum spp., Costa variabilicostata recticostata* Bold, 1970, *Orionina vaughani* group, *Paracytheridea tschoppi, Quadracythere howei, Radimella ovata,* and *Touroconcha lapidiscola* Hartmann, 1959. Ostracode assemblages such as these are found in inner-middle shelf environments today.

Ostracodes from the Escudo de Veraguas Formation (Appendix A, Map 4) are quite different from those in Cayo Agua in that there are rare to common occurrences of the ostracode taxa *Ambocythere, Argilloecia, Eucytherura, Kangarina,* macrocyprids, paracyprids, *Pseudosammocythere, Pterygocythereis, Radimella* aff. *R. ovata* Bold, 1988, and *Caudites nipeensis* Bold, 1946. In general, these taxa suggest a deeper, outer shelf environment compared to those of Cayo Agua. The ostracode evidence generally supports the interpretation of the benthic foraminiferal assemblages from these sections (Collins, 1993; Collins *et al.*, 1995).

## CORRELATION OF THE BOCAS DEL TORO AND LIMON BASIN

In order to provide a comparison between the Bocas del Toro Basin and the Limon Basin ostracode assemblages, we carried out Q- and R-mode cluster analyses using presence-absence data for 44 taxa in a small number of samples from each formation that contain representative assemblages. The Q-mode cluster analysis (Text-fig. 2a) shows samples clustering together based on shared species and reveals the following groups: Group A consists of samples mainly from the Rio Banano and Cayo Agua formations and represents ostracode assemblages characteristic of the early–middle Pliocene, roughly 2.4–5.0 Ma on the basis of planktonic foraminiferal and calcareous nannofossil biostratigraphy (Coates *et al.*, 1992). Group B consists mainly of samples from the Moin and Escudo de Veraguas formations and represents an outer shelf environment of late Pliocene and perhaps earliest Pleistocene age, about 1.6–3.0 Ma. Group C is a mixture of

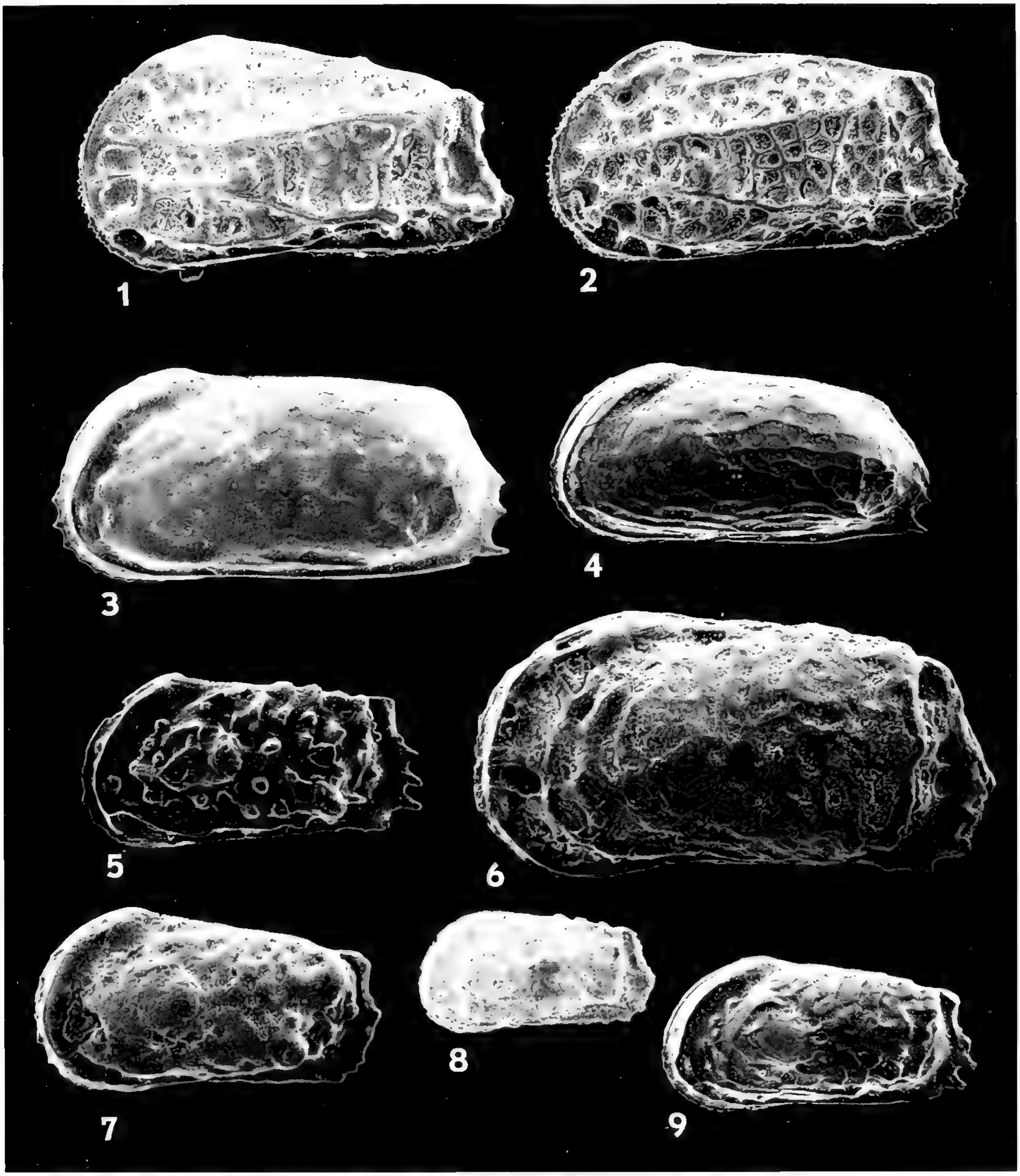


PLATE 4

1. *Orionina boldi* Cronin and Schmidt, 1981, ×120.
   LV, F, Locality PPP 710, Moin Formation, USNM 490919.
2. *Orionina vaughani* (Ulrich and Bassler, 1904), ×120.
   LV, F, Locality PPP 668, Rio Banano Formation, USNM 490920.
3. *Puriana* sp. D, ×120.
   LV, F, Locality PPP 671, Rio Banano Formation, USNM 490921.
4. *Reussicythere reussi* (Brady, 1869), ×120.
   LV, F, Locality PPP 712, Moin Formation, USNM 490922.
5. *Puriana* cf. *P. gatunensis* (Coryell and Fields, 1937), ×150.
   LV, F, Locality PPP 59, Cayo Agua Formation, USNM 490923.
6. *Coquimba fissispinata* (Benson and Coleman, 1963), ×120.
   LV, F, Locality PPP 634, Moin Formation, USNM 490924.

Table 3.—Biostratigraphic distribution of ostracode taxa, Limon Basin, Costa Rica, and Bocas del Toro Basin, Panama. Ages from Coates *et al.* (1992), Collins *et al.* (1995) and Cotton (Chapter 2, this volume).

| Species | Rio Banano Fm. 2.4–2.5 to 3.5–3.6 Ma | Moin Fm. 1.5-1.7 to 1.9 Ma | Nancy Point Fm. 5.6 to 6.5 Ma | Escudo de Veraguas Fm. 1.8–1.9 to 3.5–3.6 Ma | Caya Agua Fm. 2.9 to 4.6–5.0 Ma |
|---|---|---|---|---|---|
| *Actinocythereis gomillionensis* | X | X | | | |
| *Bradleya* aff. *B. acceptabilis* | | X | X | X | |
| *Cativella navis* | X | X | | | |
| *Caudites rectangularis* | | X | | X | X |
| *Caudites medialis* | | X | | | X |
| *Caudites nipeensis* | X | X | | X | |
| *Coquimba fissispinata* | X | X | | | |
| *Costa* cf. *C. bellipulex* | | | | X | X |
| *Echinocythereis madremastrae* | | X | | X | |
| *Hermanites hornibrooki* | | X | | | |
| *Jugosocythereis pannosa* | X | X | | | |
| *Krithe* sp. | | X | | | |
| *Costa* sp. A | X | X | | X | |
| *Orionina boldi* | | X | | | |
| *Orionina vaughani* group | X | X | | X | |
| *Puriana convoluta* | | X | | | |
| *Puriana gatunensis* | X | X | | | X |
| *Puriana minuta* | X | X | | | |
| *Puriana* aff. *P. matthewsi* | X | | | | |
| *Puriana* sp. D | X | | | | |
| *Quadracythere howei* | | X | | X | |
| *Radimella confragosa* | X | X | | X | |
| *Radimella ovata* | X | | | X | X |
| *Radimella* aff. *R. ovata* | | X | | X | |
| *Radimella wantlandi* | | X | | | |
| *Reussicythere reussi* | | X | | | |

samples from Cayo Agua, Valiente Peninsula, the southern part of Escudo de Veraguas, and part of the Rio Banano Formation. Some of these samples are considered to be early Pliocene in age (about 3.5–5.0 Ma), although there are older samples having similar biofacies. Within each of the main groups A–C, there are subclusters in which samples from the same outcrop section show a high degree of similarity because they represent similar ostracode biofacies.

The R-mode cluster analysis (Text-fig. 2b) grouped taxa that commonly occur together in the fossil assemblages. Groups 1 and 4 represent two species assemblages commonly found today inhabiting carbonate lagoon environments. Group 2 includes *Bradleya* and *Krithe* and represents the outer shelf/upper slope assemblage discussed above (Biofacies A) that may signify coastal upwelling. Group 3 is a lagoonal assemblage consisting of taxa that may prefer phytal habitats. Group 5 consists of the taxa that dominate in the Rio Banano Formation and may signify an assemblage that prefers fine-grained, muddy substrates.

## REGIONAL OSTRACODE BIOSTRATIGRAPHY

Bold (1983) summarized the stratigraphic ranges of marine and brackish water ostracodes in Cenozoic deposits from the Caribbean region based on his many years of research on assemblages from dozens of locations. More recent work on the Dominican Republic Neogene ostracode assemblages (Bold, 1988) provides additional important biostratigraphic and taxonomic data on Caribbean assemblages. Studies by Bold (1966, 1978b) showed that there are diverse ostracode

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←

7. *Puriana* cf. *P. convoluta* (Edwards, 1944), ×120.
   LV, F, Locality PPP 631, Moin Formation, USNM 490925.
8. *Puriana minuta* Bold, 1963, ×120.
   LV, F, Locality PPP 686, Rio Banano Formation, USNM 490926.
9. *Puriana* aff. *P. matthewsi* Teeter, 1975, ×120.
   LV, F, Locality PPP 712, Moin Formation, USNM 490927.

assemblages in the Limon area in the Moin and Rio Banano formations (note that Bold (1978b, Table 9) referred to the Rio Banano assemblages as "Gatun") and in Panama near the Panama Canal, but the detailed stratigraphic distributions of the species were not determined. Our work builds on Bold's biostratigraphy as we establish the stratigraphic ranges of species within the last five million years in the western Caribbean region of Central America.

Table 3 lists age diagnostic ostracode species and their occurrences in the Moin and Rio Banano formations. By calibrating the first and last stratigraphic occurrences of each species to independent age data provided by nannofossils, planktonic foraminifers, and/or paleomagnetic stratigraphy, we determined that many species are useful age markers in the study area. These diagnostic species are illustrated in Plates 1–4.

## CONCLUSIONS

The ostracodes collected from the Limon and the Bocas del Toro basins indicate that depositional environments included lagoon, carbonate platform, restricted nearshore, and outer shelf to upper slope, and, in general, the assemblages from the two regions are similar in that both contain typical extant tropical taxa. One exception to this similarity is the presence in the Moin Formation of *Bradleya* and *Krithe,* two predominantly deep-sea genera, and an *Echinocythereis* with a well-developed eye tubercle. We interpret their abundance as signifying outer shelf to upper slope environments influenced by the presence of cold, upwelling currents on the Central American continental shelf during the Late Pliocene and Early Pleistocene. This upwelling biofacies is sometimes associated with typical carbonate platform taxa, but it is not clear from the field relationships or biostratigraphy if it pre- or postdates the main Lomas del Mar reefal facies. The Lomas del Mar reef is clearly younger than the CTA Fence and Quebrada Chocolate reefs. The distinctive Rio Banano Formation ostracode assemblages at the Bomba and Quiteria sections both indicate shallow marine, clastic environments and lack typical reef or upwelling taxa. As a whole, the ostracodes from the Limon Basin indicate a great deal of temporal and spatial variability in environments of deposition over a relatively short amount of time during the Late Pliocene and Early Pleistocene.

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## CHAPTER 11

# BATHYMETRIC DISTRIBUTION OF MIOCENE TO PLEISTOCENE CARIBBEAN TELEOSTEAN FISHES FROM THE COAST OF PANAMA AND COSTA RICA

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## INTRODUCTION

Otoliths of teleostean fishes and the teeth of sharks and rays are fairly abundant in Neogene sediments of tropical America (Nolf, 1976; Gillette, 1984; Nolf and Stringer, 1992; Schwarzhans, 1993; Nolf and Aguilera, 1998). Sediment samples processed as for large microfossils commonly yield many tens to hundreds of specimens. Otoliths and teeth can be identified to genus in nearly all cases, and often to species. Detailed analyses of selected genera and families, including comparisons to specimens of living species, will result in many more taxa being identified to species. Life habits can be inferred by comparisons to living species and otolith size can be used to estimate the size of the entire fish. Thus, the natural history and food chains of the entire assemblages can be reconstructed with some confidence. Comparison with recent taxa also allows reconstruction of the bathymetry of the deposits in which the otoliths occur, which is the major focus of this paper.

Despite the great potential, there has been little systematic collecting for otoliths. To this end, we joined the Panama Paleontology Project (PPP) expedition to Bocas del Toro, Panama, in 1995, and made survey collections of most of the formations of the Bocas del Toro Group (Coates *et al.*, 1992; Coates, this volume). Subsequently, we made a preliminary survey of fishes represented in many PPP samples collected previously from the Limon Basin in Costa Rica and the Panama Canal Basin. Most of the collections examined yielded abundant, well-preserved, and diverse faunas of fossil fishes (Tables 1–5). These collections already have yielded more specimens and taxa than all previous studies from the region. The abundant occurrence and diversity of fossil fishes through time will allow, for the first time, comparison of faunal change of fishes with that of the rich record of marine benthos from tropical America.

Here, we present a preliminary analysis of the teleostean fish assemblages identified from the Caribbean coast of Panama and Costa Rica, along with their probable bathymetric distributions inferred by comparison to the bathymetric ranges of living representatives of each genus. All but two of the fossil genera are alive today in the region. We also briefly consider the occurrence of recent faunas from Eastern Pacific sediments to evaluate the potential problems of post-mortem mixing of faunas from different depths. Finally, we compare our estimates of water depths to those based on benthic foraminifera (Collins, 1993; Collins *et al.*, 1995, 1996; Collins in Jackson *et al.*, this volume).

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## MATERIAL AND METHODS

### SAMPLING

Otoliths were obtained individually from surface exposures in the field and from bulk samples. Otoliths

Table 1.—Counts of teleostean otoliths from the Gatun and Chagres formations, Panama Canal Basin, discussed in the text.

| Formation | Gatun | | | | | | | | | | | | Chagres, Rio Indio facies | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PPP numbers: | 4 | 8 | 17 | 223 | 1075 | 1973 | 2163 | 2164 | 2165 | 2166 | 2167 | 2168 | 3214 | 3215 | 3218 | 3221 | 3226 | 3225 |
| cf. *Achirus* Lacepéde, 1802 | | | | | | | | | | | | | | | | | | |
| *Albula* Scopoli, 1777 | | | | | | | | | | | | | | | | | | |
| *Anchoa* Jordan & Evermann, 1927 | | | | | | | 2 | | | | 2 | | | | | 1 | 9 | |
| *Apogon* Lacepéde, 1801 | | | | | | | | | | | 6 | 1 | 1 | 2 | | 5 | 4 | |
| *Ariosoma* Swainson, 1838 | | | | | | | | | 6 | | 2 | 5 | | | | | | |
| *Arius* Valenciennes, 1840 | 2 | | | | 1 | | | | | | | | | | | | | |
| *Bairdiella* Gill, 1862 | | | | | | | | | | | | | | | | | | |
| *Bathyclupea* Alcock, 1891 | | | | | | | | | | | | | | | | | | |
| cf. *Bembrops* Steindachner, 1876 | | | | | | | | | | | | | | | | | | |
| Bothidae, gen. indet. | | | | | | | | | | | 1 | | | | | | | |
| *Bregmaceros* Thompson, 1840 | | | | | | | 3 | | | | | 11 | 79 | 79 | 4 | 30 | 86 | |
| *Brotula* Cuvier, 1829 | | 1 | | | | | | | | | | | | | | | | |
| *Carapus* Rafinesque, 1810 | | | | | | | | | | | | | | | | | | |
| *Centropomus* Lacepéde, 1802 | | | | | | | | | | | | | | | | | | |
| *Cetengraulis* Günther, 1868 | | | | | | | | | 5 | | 1 | 65 | | | | | | |
| *Citharichthys* Bleeker, 1862 | | | | | | | 2 | | 6 | | 3 | 23 | 1 | 8 | 1 | 4 | 2 | |
| Clupeiformes | | | | | | | | | | | | | | | | | | |
| *Coelorhinchus* Gioma, 1809 | | | | | | | | | | | | | | | 1 | | | |
| Congridae, gen. indet. | | | | | | | | | | | | | | | | | | |
| cf. *Ctenosciaena* Fowler & Bean, 1924 | | 1 | | | | | | | | | | | | | | | | |
| *Cynoscion* Gill, 1862 | 3 | | | 1 | | | | | | | 2 | | | 1 | | | | |
| *Diaphus* Eigenmann & Eigenmann, 1890 | | | | | | 19 | 1 | 1 | | | 3 | 2 | 149 | 114 | 45 | 42 | 79 | 3 |
| cf. *Dicrolene* Goode & Bean, 1883 | | | | | | | | | | | | | | | | | | |
| "*Dinematichthyinorum*" | | | | | | | | | | | | | | | | | | |
| *Diplectrum* Holbrook, 1855 | | | | | | | | | | | | 5 | | | | | | |
| *Echiodon* Thompson, 1837 | | | | | | | | | | | | | | | | | | |
| *Engraulis* Cuvier, 1816 | | | | | | | 1 | | | | | | | | | | | |
| Engraulidae, gen. indet. | | | | | | | | | | | | | | | | | | |
| *Equetus* Rafinesque, 1815 | 17 | 4 | | | | | 1 | | 3 | | 6 | | | | | | | |
| *Eucinostomus* Baird & Girard, 1855 | | | | | | | | | | | | | | | | | | |
| *Gadella* Lowe, 1848 | | | | | | | | | | | | | | | | | | |
| *Genidens* (Valenciennes, 1840) | | | | | | | | | | | | | | | | | | |
| *Gephyroberyx* Boulenger, 1902 | | | | | | | | | | | | | | | | | | |
| Gerreidae, gen. indet. | | | | | | | | | | | | | | | | | | |
| Gobiidae, gen. indet. | | | | | | 2 | 23 | | 18 | 1 | 64 | 199 | 27 | 11 | | 9 | 21 | |
| Haemulidae, gen. indet. | | | | | | | 1 | | 2 | | 1 | | | | | | | |
| *Haemulon* Cuvier, 1829 | | | | | | | | 1 | | | | | | | | | | |
| *Hygophum* Bolin, 1939 | | | | | | | | | | | | | | | | | | |
| *Isopisthus* Gill, 1863 | | | | | | | | | | | | | | | | | | |
| *Lactarius* Valenciennes, 1833 | | | | | | | | | | | 1 | | | | | | 21 | |
| *Larimus* Cuvier, 1830 | 1 | | | | | | | | | | | | | | | | | |
| *Lepophidium* Gill, 1895 | | | | | | 2 | 2 | 1 | 1 | 1 | 40 | 21 | 11 | 6 | 1 | 7 | 4 | |
| *Lonchopisthus* Gill, 1862 | | | | | | 1 | 1 | | | | 11 | 3 | 6 | 2 | | 2 | 3 | |
| Lutjanidae, gen. indet. | | | | | | | | 2 | | | 3 | | | | | | | |
| *Maurolicus* Cocco, 1838 | | | | | | | | | | | | | | | | | | |

Table 1.—Continued.

| Formation | Gatun | | | | | | | | | | | | Chagres, Rio Indio facies | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PPP numbers: | 4 | 8 | 17 | 223 | 1075 | 1973 | 2163 | 2164 | 2165 | 2166 | 2167 | 2168 | 3214 | 3215 | 3218 | 3221 | 3226 | 3225 |
| Myctophidae, gen. indet. | | | | | | | | | | | | | | | | | | |
| *Myripristis* Cuvier, 1829 | | | | | | | | | | | | | | | | | | |
| *Mugil* Linnaeus, 1758 | | | | | | | | | | | | 1 | | | | | 1 | |
| *Neobythites* Goode & Bean, 1885 | | | | | | | | | | | | | | | | | | |
| *Odontoscion* Gill, 1862 | | | | | | | | | | | | | | | | | | |
| *Ophichthus* Ahl, 1789 | | | | | | | | | | | 1 | | | | | | | |
| *Ophidion* Linnaeus, 1758 | | | | | | | | | | | | | | | | | | |
| *Ophioscion* Gill, 1864 | 1 | | | | | | | | | | | | | | | | | |
| *Opistognathus* Cuvier, 1817 | | | | | | | | | | | | | | | | | | |
| *Otophidium* Gill, 1887 | | | | | | | | | | | 1 | | | | | | | |
| *Orthopristis* Girard, 1858 | | | | | | | | | | | | | | | | | | |
| *Paraconger* Kanasawa, 1961 | | | | | | | | | | | 1 | | | | | | | |
| *Paralonchurus* Bocourt, 1869 | | 1 | | | | | | | | | 1 | | | | | | | |
| *Parascombrops* Alcock, 1969 | | | | | | | | | | | | | | | | | | |
| *Plotosus* Lacepéde, 1803 | | | | | | | | | | | | | | | | | | |
| *Polyipnus* Günther, 1887 | | | | | | | | | | | | | 2 | 3 | | 2 | | |
| Pomacanthidae, gen. indet. | | | | | | | 8 | | 4 | | 1 | 13 | | | | | | |
| *Pomadasys* Lacepéde, 1802 | 1 | 1 | | | | | 4 | 2 | 5 | 3 | 50 | | | | | | | |
| *Porichthys* Girard, 1855 | | | | | | | | | | | 2 | 9 | | 2 | | | 2 | |
| *Pristigenys* Agassiz, 1835 | | | | | | | | | | | | | | | | | | |
| *Pristipomoides* Bleeker, 1852 | | | | | | | | | | | | | | | | 1 | | |
| *Pythonichthys* Poey, 1868 | | | | | | | | | | | 1 | | | | | | | |
| *Rhechias* Jordan, 1921 | | | | | | | | | | | 1 | | | | | | | |
| *Rhynchoconger* Jordan & Hubbs, 1925 | | | | | | | 1 | | | | 13 | 1 | | 1 | | 2 | 1 | |
| cf. *Rhomboplites* Gill, 1862 | | | | | | | | | 3 | | | | | | | | | |
| *Saurida* Valenciennes, 1849 | | | | | | | | | | | 1 | | | 3 | | | 3 | |
| Sciaenidae, gen. indet. | | | | | | | | | 1 | | | | | | | | | |
| *Sparisoma* Swainson, 1831 | | | | | | | | | | | | | | | | | | |
| *Serranus* Cuvier, 1816 | | | | | | | | | | | | | | | | 1 | | |
| *Stellifer* Oken, 1817 | | | | | | | | | | | | | | | | | | |
| *Steindachneria* Goode & Bean, 1888 | | | | | | | | | | | | | | | | | | |
| *Syacium* Ranzani, 1842 | | | | | | | | | | | | 2 | | | 1 | 1 | | |
| *Symphurus* (Rafinesque, 1810) | | | | | | | | | 3 | | | 5 | | 1 | | | | |
| *Trachurus* Rafinesque, 1810 | | | | | | | | | | 1 | 1 | 1 | | | | | | |
| *Umbrina* Cuvier, 1817 | 3 | | | 1 | | | | 1 | | | 3 | | | | | | | |
| *Upeneus* Cuvier, 1829 | | | | | | | | 1 | | | | | | | | | | |
| Unidentified taxa | | | | | | | 22 | | 13 | | 74 | | 372 | 345 | 120 | 100 | 63 | |
| Total Otoliths: | 28 | 7 | 1 | 2 | 1 | 24 | 70 | 9 | 70 | 6 | 289 | 367 | 648 | 578 | 173 | 207 | 299 | 3 |

Table 2.—Counts of teleostean otoliths from the Nancy Point and Shark Hole Point formations, Bocas del Toro Basin, discussed in the text.

| Formation | Nancy Point | | | | | | | | | | | | | Shark Hole Point | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PPP numbers: | 2189 | 2190 | 2194 | 2195 | 2198 | 2205 | 2206 | 2208 | 2209 | 2210 | 2211 | 2212 | 2214 | 1977 | 2202 | 2204 | 2226 | 2227 | 2228 | 2229 | 2230 |
| cf. *Achirus* Lacepéde, 1802 | | | | | | | | | | | | | | | | | | | | | |
| *Albula* Scopoli, 1777 | | | | | | | | | | | | | | | | | | | | | |
| *Anchoa* Jordan & Evermann, 1927 | | | | | | | | | | | | | | | | | | | | | |
| *Apogon* Lacepéde, 1801 | | | | | | | 1 | | | | | | | | | | 1 | | | | |
| *Ariosoma* Swainson, 1838 | | | | | | | | | | 1 | | | | | | | 1 | 1 | | | |
| *Arius* Valenciennes, 1840 | | | | | | | | | | | | | | | | | | | | | |
| *Bairdiella* Gill, 1862 | | | | | | | | | | | | | | | | | | | | | |
| *Bathyclupea* Alcock, 1891 | | | | | | | | | | | | | | | | | | | | | |
| cf. *Bembrops* Steindachner, 1876 | | | | | | | | | | | | | | | | | | | | | |
| Bothidae, gen. indet. | | | | | | | | | | | | | | | | | | | | | |
| *Bregmaceros* Thompson, 1840 | | | | | | | | 1 | 1 | | | | | | | | 1 | | | | |
| *Brotula* Cuvier, 1829 | | | | | | | | | | | | | | | | | | | | | |
| *Carapus* Rafinesque, 1810 | | | | | | | | | | | | | | | | | | | | | |
| *Centropomus* Lacepéde, 1802 | 1 | | | | | | | | | | | | | | | | | | | | |
| *Cetengraulis* Günther, 1868 | | | | | | | | | | | | | | | | | | | | | |
| *Citharichthys* Bleeker, 1862 | | | | | | | 1 | | | | | | | | | | | | | | |
| Clupeiformes | | | | | | | | | | | | | | | | | | | | | |
| *Coelorhinchus* Gioma, 1809 | | | | | | | | | | | | | | | | | | | | | |
| Congridae, gen. indet. | | | | | | | | | | | | | | | | | | | | | |
| cf. *Ctenosiaena* Fowler & Bean, 1924 | | | | | | | | | | | | | | | | | | | | | |
| *Cynoscion* Gill, 1862 | | | | | | | | | | | | | | | | | | | | | |
| *Diaphus* Eigenmann & Eigenmann, 1890 | 13 | 5 | | 1 | | | 91 | 7 | | 1 | 7 | 8 | 2 | | 2 | 4 | 3 | 11 | 7 | 4 | 1 |
| cf. *Dicrolene* Goode & Bean, 1883 | | | | | | | | | | | | | | | | | | | | | |
| "*Dinematichthyinorum*" | | | | | | | | | | | | | | | | | | | | | |
| *Diplectrum* Holbrook, 1855 | | | | | | | | | | | | | | | | | | | | | |
| *Echiodon* Thompson, 1837 | | | | | | | | | | | | | | | | | | | | | |
| *Engraulis* Cuvier, 1816 | | | | | | | | | | | | | | | | | | | | | |
| Engraulidae, gen. indet. | | | | | | | | | | | | | | | | | | | | | |
| *Equetus* Rafinesque, 1815 | | | | | | | | | | | | | | | | | | | | | |
| *Eucinostomus* Baird & Girard, 1855 | | | | | | | 1 | | | | | | | | | | | | | | |
| *Gadella* Lowe, 1848 | | | | | | | | | | | | | | | | | | | | | |
| *Genidens* (Valenciennes, 1840) | | | | | | | | | | | | | | 1 | | | | | | | |
| *Gephyroberyx* Boulenger, 1902 | | | | | | | | | | | | | | | | | | | | | |
| Gerreidae, gen. indet. | | | | | | | 1 | | | | | | | | | | | | | | |
| Gobiidae, gen. indet. | | | 1 | | | | 7 | 1 | | | | | | | | | 1 | | | | |
| Haemulidae, gen. indet. | | | | | | | | | | | | | | | | | | | | | |
| *Haemulon* Cuvier, 1829 | | | | | | | | | | | | | | | | | | | | | |
| *Hygophum* Bolin, 1939 | | | | | | | | | | | | | | | | | | | | | |
| *Isopisthus* Gill, 1863 | | | | | | | | | | | | | | | | | | | | | |
| *Lactarius* Valenciennes, 1833 | | | | | | | 1 | | | | | | | | | | 1 | | | | |
| *Larimus* Cuvier, 1830 | | | | | | | | | | | | | | | | | | | | | |
| *Lepophidium* Gill, 1895 | | | | | | | 1 | 2 | | | | | 1 | | | | 1 | | | | |
| *Lonchopisthus* Gill, 1862 | | | | | | | | | | | | | | | | | | | | | |
| Lutjanidae, gen. indet. | | | | | | | | | | | | | | | | | | | | | |

Table 2.—Continued.

| Formation | Nancy Point | | | | | | | | | | | | | Shark Hole Point | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PPP numbers: | 2189 | 2190 | 2194 | 2195 | 2198 | 2205 | 2206 | 2208 | 2209 | 2210 | 2211 | 2212 | 2214 | 1977 | 2202 | 2204 | 2226 | 2227 | 2228 | 2229 | 2230 |
| *Maurolicus* Cocco, 1838 | | | | | | | | | | | | | | | | | | | | | |
| Myctophidae, gen. indet. | 5 | | | 1 | 1 | 1 | | | | | | | | | | | 2 | 1 | | | |
| *Myripristis* Cuvier, 1829 | | | | | | | | | | | | | | | | | | | | | |
| *Mugil* Linnaeus, 1758 | | | | | | | | | | | | | | | | | | | | | |
| *Neobythites* Goode & Bean, 1885 | 1 | | | | | | | | | | | | | | | | | | | 2 | |
| *Odontoscion* Gill, 1862 | | | | | | | | | | | | | | | | | | | | | |
| *Ophichthus* Ahl, 1789 | | | | | | | | | | | | | | | | | | | | | |
| *Ophidion* Linnaeus, 1758 | | | | | | | | | | | | | | | | | | | | | |
| *Ophioscion* Gill, 1864 | | | | | | | | | | | | | | | | | | | | | |
| *Opistognathus* Cuvier, 1817 | | | | | | | | | | | | | | | | | | | | | |
| *Otophidium* Gill, 1887 | | | | | | | | | | | | | | | | | | | | | |
| *Orthopristis* Girard, 1858 | | | | | | | | | | | | | | | | | | | | | |
| *Paraconger* Kanasawa, 1961 | | | | | | | | | | | | | | | | | | | | | |
| *Paralonchurus* Bocourt, 1869 | | | | | | | | | | | | | | | | | | | | | |
| *Parascombrops* Alcock, 1969 | | | | 1 | | | | | | | | | | | | | 1 | 1 | 1 | | |
| *Plotosus* Lacepéde, 1803 | | | | | | | | | | | | | | | | | | | | | |
| *Polyipnus* Günther, 1887 | | | | | | | 1 | | | | | | | | | | | | | | |
| Pomacanthidae, gen. indet. | | | | | | | | | | | | | | | | | | | | | |
| *Pomadasys* Lacepéde, 1802 | | | | | | | | | | | | | | | | | | | | | |
| *Porichthys* Girard, 1855 | | | | | | | | | | | | | | | | | | | | | |
| *Pristigenys* Agassiz, 1835 | | | | | | | | | | | | | | | | | | | | | |
| *Pristipomoides* Bleeker, 1852 | | | | | | | | | | | | | | | | | | | | | |
| *Pythonichthys* Poey, 1868 | | | | | | | | | | | | | | | | | | | | | |
| *Rhechias* Jordan, 1921 | | | | | | | | | | | | | | | | | | | | | |
| *Rhynchoconger* Jordan & Hubbs, 1925 | | | | | | | 1 | | | | 1 | | | | | | | | | | |
| cf. *Rhomboplites* Gill, 1862 | | | | | | | | | | | | | | | | | | | | | |
| *Saurida* Valenciennes, 1849 | | | | | | | | | | | | | | | | | | | | | |
| Sciaenidae, gen. indet. | | | | | | | | | | | | | | | | | | | | | |
| *Sparisoma* Swainson, 1831 | | | | | | | | | | | | | | | | | | | | | |
| *Serranus* Cuvier, 1816 | | | | | | | | | | | | | | | | | | | | | |
| *Stellifer* Oken, 1817 | | | | | | | | | | | | | | | | | | | | | |
| *Steindachneria* Goode & Bean, 1888 | | | 1 | | | | | | | | | | | | | 1 | | | | | |
| *Syacium* Ranzani, 1842 | | | | | | | | | | | | | | | | | | | | | |
| *Symphurus* (Rafinesque, 1810) | | | | | | | | | | | | | | | | | | | | | |
| *Trachurus* Rafinesque, 1810 | | | | | | | 1 | | | | | | | | | | | | | | |
| *Umbrina* Cuvier, 1817 | | | | | | | 1 | | | | | | | | | | | | | | |
| *Upeneus* Cuvier, 1829 | | | | | | | | | | | | | | | | | | | | | |
| Unidentified taxa | 1 | 1 | | | | | | 3 | | | | | | | | | | | | | 2 |
| Total Otoliths: | 21 | 6 | 1 | 4 | 1 | 1 | 108 | 14 | 1 | 2 | 8 | 8 | 3 | 1 | 2 | 5 | 12 | 14 | 8 | 6 | 3 |

Table 3.—Counts of teleostean otoliths from the Cayo Agua and Swan Cay formations, Bocas del Toro Basin, discussed in the text.

| Formation | Cayo Agua | | | | | | | | | | | | | Swan Cay | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PPP numbers: | 1188 | 2222 | 2224 | 2225 | 2232 | 2234 | 2235 | 2236 | 2237 | 2238 | 2239 | 2242 | 2245 | 1995 | 2221 | 2246 | 2531 |
| cf. *Achirus* Lacepéde, 1802 | 1 | | | | | | | | | | | | | | | | |
| *Albula* Scopoli, 1777 | | | | | | | 1 | | | | | | | | | | |
| *Anchoa* Jordan & Evermann, 1927 | 8 | | | 1 | | 1 | | | 5 | | | | | | | | |
| *Apogon* Lacepéde, 1801 | 18 | | | 2 | | | 1 | | | | 1 | | 1 | 47 | 138 | 75 | 114 |
| *Ariosoma* Swainson, 1838 | 28 | 1 | 3 | 2 | 1 | | 4 | 11 | 2 | | | 1 | | 3 | 11 | 32 | 3 |
| *Arius* Valenciennes, 1840 | 1 | | | | | | | | | | | | | | | | |
| *Bairdiella* Gill, 1862 | | | | | | | | | | | | | | | | | |
| *Bathyclupea* Alcock, 1891 | | | | | | | | | | | | | | | | | |
| cf. *Bembrops* Steindachner, 1876 | | | | | | | | | | | | | | | | | |
| Bothidae, gen. indet. | 5 | | 4 | | | | | | | | | | | | 5 | | 2 |
| *Bregmaceros* Thompson, 1840 | 7 | | 1 | | | 1 | | | | | | | | 92 | 54 | 385 | 48 |
| *Brotula* Cuvier, 1829 | | | | | | | | | | | | | | 1 | 6 | 1 | 6 |
| *Carapus* Rafinesque, 1810 | 1 | | | | | | | | | | | | | | | | |
| *Centropomus* Lacepéde, 1802 | 1 | | | | | | | | | | | | | | | 1 | |
| *Cetengraulis* Günther, 1868 | 11 | | | | 1 | | | 1 | 2 | | 1 | | | | | | |
| *Citharichthys* Bleeker, 1862 | 21 | | 2 | | 1 | | 2 | 1 | 7 | | | | 1 | 1 | | | 3 |
| Clupeiformes | | | | | | | | | 4 | | | | | | | 1 | |
| *Coelorhinchus* Gioma, 1809 | | | | | | | | | | | | | | | | | |
| Congridae, gen. indet. | | | | | | | | | | | | | | | 2 | | 1 |
| cf. *Ctenosciaena* Fowler & Bean, 1924 | 1 | | | | | | | | | | | | | | | | |
| *Cynoscion* Gill, 1862 | | | | | | | | | | | | | | | | | |
| *Diaphus* Eigenmann & Eigenmann, 1890 | 51 | 5 | 28 | 43 | | 1 | 11 | 5 | 4 | | | | | 1 | 81 | 6 | 4 |
| cf. *Dicrolene* Goode & Bean, 1883 | | | | | | | | | | | | | | | | | |
| "*Dinematichthyinorum*" | | | | | | | | | | | | | | | 11 | | 5 |
| *Diplectrum* Holbrook, 1855 | | | | 1 | | | | | | | | | | | | | |
| *Echiodon* Thompson, 1837 | | | | | | 1 | | | | | | | | | 6 | | 5 |
| *Engraulis* Cuvier, 1816 | | | | | | | | | | | | | | | | | |
| Engraulidae, gen. indet. | 10 | | | | | 2 | | | 5 | | | | | | | | |
| *Equetus* Rafinesque, 1815 | | | | | | | | | | | | | | | | | |
| *Eucinostomus* Baird & Girard, 1855 | 1 | | | | | | | | 1 | | | | | | | | |
| *Gadella* Lowe, 1848 | | | | | | | | | | | | | | | 40 | | 37 |
| *Genidens* (Valenciennes, 1840) | | | | | | | | | | | | | | | | | |
| *Gephyroberyx* Boulenger, 1902 | | | | | | | | | | | | | | | | | |
| Gerreidae, gen. indet. | | | 1 | | | | | | | | | | | | | | |
| Gobiidae, gen. indet. | 67 | 5 | | 9 | | 3 | 5 | 4 | 9 | 2 | 2 | | | 10 | 45 | 128 | 17 |
| Haemulidae, gen. indet. | | | | | | | | | | | | | | | | 1 | |
| *Haemulon* Cuvier, 1829 | 2 | 1 | | | | | | | | | | | | 1 | | 2 | |
| *Hygophum* Bolin, 1939 | | | | 1 | | 1 | | | | | | | | | 1 | | |
| *Isopisthus* Gill, 1863 | | | | | | | | | | | | | | | | | |
| *Lactarius* Valenciennes, 1833 | | | | | | | | | 1 | | | | | | | | |
| *Larimus* Cuvier, 1830 | 1 | | | 1 | | | | | 2 | | | | | | | | |
| *Lepophidium* Gill, 1895 | 24 | 3 | 2 | 5 | | | 13 | 5 | 4 | | | 1 | | 2 | 3 | 12 | 1 |
| *Lonchopisthus* Gill, 1862 | 3 | 1 | | 4 | | | | | | | | | | | 2 | 4 | |
| Lutjanidae, gen. indet. | | | | | | | 1 | | | | | | | 1 | | 1 | |
| *Maurolicus* Cocco, 1838 | | | | | | | | | | | | | | | | | |

Table 3.—Continued.

| Formation | Cayo Agua | | | | | | | | | | | | | Swan Cay | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PPP numbers: | 1188 | 2222 | 2224 | 2225 | 2232 | 2234 | 2235 | 2236 | 2237 | 2238 | 2239 | 2242 | 2245 | 1995 | 2221 | 2246 | 2531 |
| Myctophidae, gen. indet. | 6 | | 1 | | | 2 | | 2 | | | | | | | | | |
| *Myripristis* Cuvier, 1829 | | | | | | | | | | | | | | | 3 | | |
| *Mugil* Linnaeus, 1758 | | | | | | | | | | | | | | | | | |
| *Neobythites* Goode & Bean, 1885 | 2 | | | | | | | | | | | | | | 1 | | 2 |
| *Odontoscion* Gill, 1862 | | | | | | | | | | | | | | | | | |
| *Ophichthus* Ahl, 1789 | | | | | | | | | | | | | | | | | |
| *Ophidion* Linnaeus, 1758 | | | | | | | | | | | | | | 8 | 14 | | 17 |
| *Ophioscion* Gill, 1864 | | | | | | | | | | | | | | | | | |
| *Opistognathus* Cuvier, 1817 | 1 | | | | | | | | | | | | | | | | |
| *Otophidium* Gill, 1887 | 3 | | | | | | | | 1 | | | | | 1 | | | |
| *Orthopristis* Girard, 1858 | 1 | | | | | | | | | | | | | | | | |
| *Paraconger* Kanasawa, 1961 | | | | | | | | | | | | | | | | | |
| *Paralonchurus* Bocourt, 1869 | | | | | | | | | | | | | | | | | |
| *Parascombrops* Alcock, 1969 | 6 | | | | | | 1 | 1 | | | | | | 70 | 226 | 18 | 88 |
| *Plotosus* Lacepéde, 1803 | 1 | | | | | | | | | | | | | | | 1 | |
| *Polyipnus* Günther, 1887 | 1 | | | | | | | | | | | | | | 9 | | |
| Pomacanthidae, gen. indet. | | | | | | | | | | | | | | | | | |
| *Pomadasys* Lacepéde, 1802 | | | | | | | | | | | | | | | | | |
| *Porichthys* Girard, 1855 | 3 | | | | 1 | | 1 | | 4 | | | | | | 12 | 4 | 3 |
| *Pristigenys* Agassiz, 1835 | 1 | | | | | | | | | | | | | | 1 | | |
| *Pristipomoides* Bleeker, 1852 | 1 | | | 1 | | | | | | | | | | | 4 | | 2 |
| *Pythonichthys* Poey, 1868 | | | | | | | | | | | | | | | | 1 | |
| *Rhechias* Jordan, 1921 | | | | | | | | | | | | | | | | | |
| *Rhynchoconger* Jordan & Hubbs, 1925 | 2 | 1 | 9 | 20 | | | | | | | | | | 2 | 33 | 7 | 6 |
| cf. *Rhomboplites* Gill, 1862 | 1 | | | | | | | | | | | | | | | | |
| *Saurida* Valenciennes, 1849 | | | | | | | | | 1 | | | | | | | 12 | |
| Sciaenidae, gen. indet. | | | | | | | | | | | | | | | | | |
| *Sparisoma* Swainson, 1831 | | | | | | | | | | | | | | | | | |
| *Serranus* Cuvier, 1816 | | | | | | | | | | | | | | | | 1 | |
| *Stellifer* Oken, 1817 | | | | | | | | | | | | | | | | | |
| *Steindachneria* Goode & Bean, 1888 | 1 | | | | | | | 1 | 1 | | | | | | | | |
| *Syacium* Ranzani, 1842 | 1 | | | | | | 1 | | | | | | | 1 | | | |
| *Symphurus* (Rafinesque, 1810) | | | | | | | | | 1 | | | | | | 1 | | 2 |
| *Trachurus* Rafinesque, 1810 | | | | | | | | | | | | | | | | | |
| *Umbrina* Cuvier, 1817 | 1 | | | 4 | | | | 1 | | | | | | | | | |
| *Upeneus* Cuvier, 1829 | | | | | | | | | | | | | | | | | |
| Unidentified taxa | 45 | 1 | 17 | 3 | | | 12 | 2 | 13 | | 1 | | | 3 | 107 | 78 | 92 |
| Total Otoliths: | 338 | 18 | 68 | 97 | 4 | 12 | 53 | 34 | 67 | 2 | 5 | 2 | 2 | 244 | 816 | 771 | 458 |

Table 4.—Counts of teleostean otoliths from the Escudo de Veraguas , Bocas del Toro Basin, Formation discussed in the text.

| Formation | Escudo de Veraguas | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PPP numbers: | 178 | 1241 | 1245 | 2169 | 2170 | 2171 | 2172 | 2173 | 2175 | 2176 | 2177 | 2178 | 2179 | 2181 | 2182 | 2183 | 2184 | 2185 | 2186 | 2187 |
| cf. *Achirus* Lacepéde, 1802 | | | | | | | | | | | | | | | | | | | | |
| *Albula* Scopoli, 1777 | | 12 | | 2 | | | | 1 | | | 1 | | | | | | | | | |
| *Anchoa* Jordan & Evermann, 1927 | | | | | | | | | | | | | | | | | | | | |
| *Apogon* Lacepéde, 1801 | | | | | 42 | | | 1 | 1 | | 2 | 1 | 1 | 1 | | | 4 | | | 3 |
| *Ariosoma* Swainson, 1838 | | 3 | | 5 | 1 | | | | | | | | | | | | 1 | | | 3 |
| *Arius* Valenciennes, 1840 | | | | | | | | | | | | | | | | | 1 | | | |
| *Bairdiella* Gill, 1862 | | | | | | | | | | | | | | | | | | | | |
| *Bathyclupea* Alcock, 1891 | | 1 | | | | | | | | | | | | | | | | | | |
| cf. *Bembrops* Steindachner, 1876 | | | | | 1 | | | | | | | | | | | | | | | |
| Bothidae, gen. indet. | | 1 | | | | | | | | | | | | | | | | | | |
| *Bregmaceros* Thompson, 1840 | | 33 | | 6 | 166 | | | | | | | | | | 1 | | | | | |
| *Brotula* Cuvier, 1829 | | | | | | | | | | | | | | | | | | | | |
| *Carapus* Rafinesque, 1810 | | | | | | | | | | | | | | | | | | | | |
| *Centropomus* Lacepéde, 1802 | | | | | | | | | | | | | | | | | | | | |
| *Cetengraulis* Günther, 1868 | | | | | | | | | | | | | | | | | | | | |
| *Citharichthys* Bleeker, 1862 | | 4 | | | | | | | | | | | | | | | | | | |
| Clupeiformes | | | | | | | | | | | | | | | | | | | | |
| *Coelorhinchus* Gioma, 1809 | | | | | | | | | | | | | | | | | | | | |
| Congridae, gen. indet. | | | | | | | | | | | | | | | | | | | | |
| cf. *Ctenosciaena* Fowler & Bean, 1924 | | | | | | | | | | | | | | | | | | | | |
| *Cynoscion* Gill, 1862 | | | | | 1 | | | | | | | | | | | | | 1 | | |
| *Diaphus* Eigenmann & Eigenmann, 1890 | | | | | | | | | | | | | | | | | | | | |
| cf. *Dicrolene* Goode & Bean, 1883 | 5 | 31 | | 31 | 17 | 4 | 1 | 1 | | 8 | 6 | 9 | | 2 | 5 | 5 | 40 | | | 8 |
| "*Dinematichthyinorum*" | | | | | | | | | | | | | | | | | | | | 1 |
| *Diplectrum* Holbrook, 1855 | | | | | 8 | | | | | | | | | | | | | | | |
| *Echiodon* Thompson, 1837 | | | | | | | | | | | | | | | | | | | | |
| *Engraulis* Cuvier, 1816 | | | | | | | | | | | | | | | | | | | | |
| Engraulidae, gen. indet. | | | | | | | | | | | | | | | | | | | | |
| *Equetus* Rafinesque, 1815 | | | | | | | | | | | | | | | | | | | | |
| *Eucinostomus* Baird & Girard, 1855 | | | | | | | | | | | | | | | | | | | | |
| *Gadella* Lowe, 1848 | | | | | 1 | | | | | | | | | | | | 1 | | | |
| *Genidens* (Valenciennes, 1840) | | | | | | | | | | | | | | | | | | | | |
| *Gephyroberyx* Boulenger, 1902 | | | | | 1 | | | | | | | | | | | | | | | |
| Gerreidae, gen. indet. | | | | | | | | | | | | | | | | | 1 | | | |
| Gobiidae, gen. indet. | | 22 | | 3 | 61 | 1 | 1 | 1 | 2 | 2 | | | | | 1 | | 6 | | | 1 |
| Haemulidae, gen. indet. | | | | | | | | | | | | | | | | | 2 | | | |
| *Haemulon* Cuvier, 1829 | | | | | | | | | | | | | | | | | | | | |
| *Hygophum* Bolin, 1939 | | | | | 1 | | | | | | | | | | | 1 | | | | |
| *Isopisthus* Gill, 1863 | | | | | | | | | | | | | | | | | | | | |
| *Lactarius* Valenciennes, 1833 | | | | | | | | | | | | | | | | | | | | |
| *Larimus* Cuvier, 1830 | | | | | | | | | | | | | | | | | | | | |
| *Lepophidium* Gill, 1895 | | 2 | | 3 | 5 | | | | | | | 2 | | 1 | | | 3 | | | |
| *Lonchopisthus* Gill, 1862 | | 2 | | | | | | | 1 | | 1 | | | 2 | | | 1 | | 1 | 2 |
| Lutjanidae, gen. indet. | 1 | | | 1 | 1 | | | | | | | | | | | | | | | |
| *Maurolicus* Cocco, 1838 | | | | | 1 | | | | | | | | | | | | | | | 1 |

Table 4.—Continued.

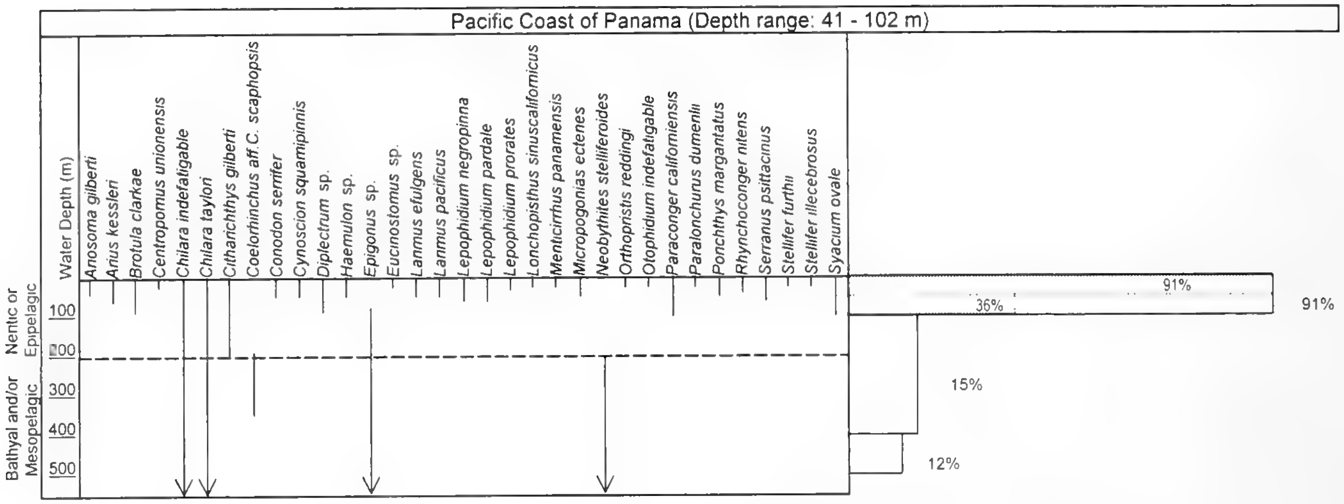
| Formation | Escudo de Veraguas | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PPP numbers: | 178 | 1241 | 1245 | 2169 | 2170 | 2171 | 2172 | 2173 | 2175 | 2176 | 2177 | 2178 | 2179 | 2181 | 2182 | 2183 | 2184 | 2185 | 2186 | 2187 |
| Myctophidae, gen. indet. | | | | | | | | | | | | | | | | | 1 | | | |
| *Myripristis* Cuvier, 1829 | | | | | | | | | | | | | | | | | | | | |
| *Mugil* Linnaeus, 1758 | | | | | | | | | | | | | | | | | | | | |
| *Neobythites* Goode & Bean, 1885 | | | | | | | | | | | | | | | | | | | | |
| *Odontoscion* Gill, 1862 | | | | | | | | | | | | | | | | | | | | |
| *Ophichthus* Ahl, 1789 | | | | | | | | | | | | | | | | | | | | |
| *Ophidion* Linnaeus, 1758 | | | | | | | | | | | | | | | | | | | | |
| *Ophioscion* Gill, 1864 | | | | | | | | | | | | | | | | | | | | |
| *Opistognathus* Cuvier, 1817 | | | | | | | | | | | | | | | | | | | | |
| *Otophidium* Gill, 1887 | | | | | | | | | | | | | | | | | | | | |
| *Orthopristis* Girard, 1858 | | | | | | | | | | | | | | | | | | | | |
| *Paraconger* Kanasawa, 1961 | | | | | | | | | | | | | | | | | | | | |
| *Paralonchurus* Bocourt, 1869 | | | | | | | | | | | | | | | | | 1 | | | |
| *Parascombrops* Alcock, 1969 | | 24 | | 3 | 60 | | | | | 2 | 1 | | 1 | | | | 2 | | | 2 |
| *Piotosus* Lacepéde, 1803 | | | | | | | | | | | | | | | | | | | | |
| *Polyipnus* Günther, 1887 | | 10 | 1 | | 12 | | | | | | | 1 | | | | | | | | 1 |
| Pomacanthidae, gen. indet. | | | | | | | | | | | | | | | | | | | | |
| *Pomadasys* Lacepéde, 1802 | | | | | | | | | | | | | | | | | 2 | | | |
| *Porichthys* Girard, 1855 | | 5 | | 3 | | | | | | | | | | 1 | 1 | | 1 | | | |
| *Pristigenys* Agassiz, 1835 | | | | | | | | | | | | | | | | | | | | |
| *Pristipomoides* Bleeker, 1852 | | | | 1 | 6 | | | 1 | | | 1 | | | | | | 4 | | | 3 |
| *Pythonichthys* Poey, 1868 | | | | | | | | | | | | | | | | | | | | |
| *Rhechias* Jordan, 1921 | | | | | | | | | | | | | | | | | | | | |
| *Rhynchoconger* Jordan & Hubbs, 1925 | | 7 | | 2 | 2 | 2 | | | | 25 | | | | | | | 1 | | | 3 |
| cf. *Rhomboplites* Gill, 1862 | | | | | | | | | | | | | | | | | | | | |
| *Saurida* Valenciennes, 1849 | | | | | 2 | | | | | | | | | | | | 2 | | | 2 |
| Sciaenidae, gen. indet. | | | | | | | | | | | | | | | | | 3 | | | |
| *Sparisoma* Swainson, 1831 | | | | | | | | | | | | | | 1 | | | | | | |
| *Serranus* Cuvier, 1816 | | | | | | | | | | | | | | | | | | | | |
| *Stellifer* Oken, 1817 | | | | | | | | | | | | | | | | | | | | |
| *Steindachneria* Goode & Bean, 1888 | | | | | | | | 1 | | | | | | 1 | | | | | | |
| *Syacium* Ranzani, 1842 | | 1 | | | | | | | | | | | | | | | | | | |
| *Symphurus* (Rafinesque, 1810) | | | | | | | | | | | | | | | | | | | | |
| *Trachurus* Rafinesque, 1810 | | | | | | | | | | | | | | | | | | | | 1 |
| *Umbrina* Cuvier, 1817 | | | | | | | | | | | | | | | | | | | | |
| *Upeneus* Cuvier, 1829 | | | | | | | | | | | | | | | | | | | | |
| Unidentified taxa | | 25 | | 12 | 46 | | | | | | | 1 | | | | 1 | 3 | | | 4 |
| Total Otoliths: | 6 | 183 | 1 | 72 | 435 | 7 | 2 | 6 | 4 | 37 | 12 | 14 | 2 | 9 | 8 | 7 | 80 | 1 | 1 | 35 |

Table 5.—Counts of teleostean otoliths from the Uscari, Rio Banano, Limon Basin, formations, and Moin discussed in the text.

| Formation | Uscari | | | Rio Banano | | | | | | | Moin | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PPP numbers: | 1736 | 1768 | 1770 | 1726 | 1727 | 1728 | 1731 | 1732 | 1734 | 1735 | 944 | 948 | 950 | 963 | 2024 | 2032 | 2038 |
| cf. *Achirus* Lacepéde, 1802 | | | | | | | | | | | | | | | | | |
| *Albula* Scopoli, 1777 | | | | | | | | 1 | | | | | | | | 1 | |
| *Anchoa* Jordan & Evermann, 1927 | | | | | | | | | | | | | | | | | |
| *Apogon* Lacepéde, 1801 | | | | | 7 | | | | | | | | | 3 | 1 | 13 | 21 |
| *Ariosoma* Swainson, 1838 | | | | | 1 | 1 | | | | | | | | | | 413 | 4 |
| *Arius* Valenciennes, 1840 | | | | | | | | | | | | | | | | | |
| *Bairdiella* Gill, 1862 | | | | | 1 | | | | | | | | | | | | |
| *Bathyclupea* Alcock, 1891 | | | | | | | | | | | | | | | | | |
| cf. *Bembrops* Steindachner, 1876 | | | | | | | | | | | | | | | | | |
| Bothidae, gen. indet. | | | | | | | | | | | | | | | | | |
| *Bregmaceros* Thompson, 1840 | | | | | | | | | | | | | | | 1 | 23 | 11 |
| *Brotula* Cuvier, 1829 | | | | | | | | | | | | | | | | | |
| *Carapus* Rafinesque, 1810 | | | | | | | | | | | | | | | | | |
| *Centropomus* Lacepéde, 1802 | | | | | | | | | | | | | | | | | |
| *Cetengraulis* Günther, 1868 | | | | | | | | | | | | | | | | | |
| *Citharichthys* Bleeker, 1862 | | | | | | | | | | | | | | | | | |
| Clupeiformes | | | | | | | | | | | | | | | | | |
| *Coelorhinchus* Gioma, 1809 | | | | | | | | | | | | | | | | | |
| Congridae, gen. indet. | | | | | | | | | | | | | | | | | |
| cf. *Ctenosciaena* Fowler & Bean, 1924 | | | | | | | | 1 | | | | | | | | | |
| *Cynoscion* Gill, 1862 | | | | | 2 | 3 | 1 | | 1 | 1 | | | | | | | |
| *Diaphus* Eigenmann & Eigenmann, 1890 | 1 | 5 | 2 | | | 1 | | 2 | | 1 | 7 | | 27 | 15 | 6 | 30 | 77 |
| cf. *Dicrolene* Goode & Bean, 1883 | | | | | | | | | | | | | | | | | |
| "*Dinematichthyinorum*" | | | | | | | | | | | | | | | | | 2 |
| *Diplectrum* Holbrook, 1855 | | | | | | | | | | | | | | | | | 1 |
| *Echiodon* Thompson, 1837 | | | | | | | | | | | | | | | | | |
| *Engraulis* Cuvier, 1816 | | | | | 1 | | | | | | | | | | | | |
| Engraulidae, gen. indet. | | | | | | | | | | | | | | | | | |
| *Equetus* Rafinesque, 1815 | | | | | | | | | | | | | | | | | |
| *Eucinostomus* Baird & Girard, 1855 | | | | 1 | | 2 | | 1 | | 1 | | | | | | | |
| *Gadella* Lowe, 1848 | | | | | | | | | | | | | | | | | 3 |
| *Genidens* (Valenciennes, 1840) | | | | | | | | | | | | | | | | | |
| *Gephyroberyx* Boulenger, 1902 | | | | | | | | | | | | | | | | | |
| Gerreidae, gen. indet. | | | | | | | | | | | | | | | | | |
| Gobiidae, gen. indet. | | | | | | | | 11 | | | | | | | | | 9 |
| Haemulidae, gen. indet. | | | | | | | | | | | | | 1 | | | | |
| *Haemulon* Cuvier, 1829 | | | | | | | | | | 1 | | | | | | | |
| *Hygophum* Bolin, 1939 | | | | | | | | | | | | | | | | | |
| *Isopisthus* Gill, 1863 | | | | | 4 | | | | | | | | | | | | |
| *Lactarius* Valenciennes, 1833 | | | | 2 | | | | | | | | | | | | | |
| *Larimus* Cuvier, 1830 | | | | 2 | 4 | 1 | | 2 | 2 | | | | | | | | |
| *Lepophidium* Gill, 1895 | | | | | 1 | 1 | | | | | 1 | | | | | 5 | 3 |
| *Lonchopisthus* Gill, 1862 | | | | | | | | | | | | | | | | | 1 |
| Lutjanidae, gen. indet. | | | | | | | | | | | | | | | | | |
| *Maurolicus* Cocco, 1838 | | | | | | | | | | | | | | | | | |

Table 5.—Continued.

| Formation | Uscari | | | Rio Banano | | | | | | | Moin | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PPP numbers: | 1736 | 1768 | 1770 | 1726 | 1727 | 1728 | 1731 | 1732 | 1734 | 1735 | 944 | 948 | 950 | 963 | 2024 | 2032 | 2038 |
| Myctophidae, gen. indet. | | | | | | | | | | | | | | | | | |
| *Myripristis* Cuvier, 1829 | | | | | | | | | | | | | | | | | |
| *Mugil* Linnaeus, 1758 | | | | | | | | | | | | | | | | | |
| *Neobythites* Goode & Bean, 1885 | | | | | | | | | | | | | | | | | 1 |
| *Odontoscion* Gill, 1862 | | | | | | | | | 1 | | | | | | | | |
| *Ophichthus* Ahl, 1789 | | | | | | | | | | | | | | | | | |
| *Ophidion* Linnaeus, 1758 | | | | | | | | | | | | | | | | | |
| *Ophioscion* Gill, 1864 | | | | | | | | | | | | | | | | | |
| *Opistognathus* Cuvier, 1817 | | | | | | | | | | | | | | | | | 1 |
| *Otophidium* Gill, 1887 | | | | | | | | | | | | | | | | | |
| *Ortopristis* Girard, 1858 | | | | | | | | | | | | | | | | | |
| *Paraconger* Kanasawa, 1961 | | | | | | | | | | | | | | | | 4 | |
| *Paralonchurus* Bocourt, 1869 | | | | | 1 | 1 | | | | | | | | | | | |
| *Parascombrops* Alcock, 1969 | | | | | | | | | | | | | | 1 | | 1 | 2 |
| *Plotosus* Lacepéde, 1803 | | | | | | | | | | | | | | | | | |
| *Polyipnus* Günther, 1887 | | | | | | | | | | | | | | | | | |
| Pomacanthidae, gen. indet. | | | | | | | | | | | | | | | | | |
| *Pomadasys* Lacepéde, 1802 | | | | | | | | | | | | | | | | | |
| *Porichthys* Girard, 1855 | | | | | 1 | | | | | | | | | | | 1 | |
| *Pristigenys* Agassiz, 1835 | | | | | | | | | | | | | | | | | |
| *Pristipomoides* Bleeker, 1852 | | | | | | | | | | | | | | | | | 3 |
| *Pythomichthys* Poey, 1868 | | | | | | | | | | | | | | | | | |
| *Rhechias* Jordan, 1921 | | | | | | | | | | | | | | | | | |
| *Rhynchoconger* Jordan & Hubbs, 1925 | | | | | | | 1 | | | 1 | | 1 | | | | | 2 |
| cf. *Rhomboplites* Gill, 1862 | | | | | | | | | | | | | | | | | |
| *Saurida* Valenciennes, 1849 | | | | | | | | | | | | | | | | | |
| Sciaenidae, gen. indet. | | | | | 2 | | | | | | | | | | | | 1 |
| *Sparisoma* Swainson, 1831 | | | | | | | | | | | | | | | | | |
| *Serranus* Cuvier, 1816 | | | | | | | | | | | | | | | | | |
| *Stellifer* Oken, 1817 | | | | | 4 | 1 | | | | | | | | | | | |
| *Steindachneria* Goode & Bean, 1888 | | | | | | | | | | | | | 1 | | | 2 | |
| *Syacium* Ranzani, 1842 | | | | | | | | | | | | | | | | | |
| *Symphurus* (Rafinesque, 1810) | | | | | | | | | | | | | | | | | |
| *Trachurus* Rafinesque, 1810 | | | | | | | | | | | | | | | | | |
| *Umbrina* Cuvier, 1817 | | | | | | 1 | | 2 | | | | | | | | | |
| *Upeneus* Cuvier, 1829 | | | | | | | | | | | | | | | | | |
| Unidentified taxa | | | | | | | | | | | | | | | | 46 | 16 |
| Total Otoliths: | 1 | 5 | 2 | 5 | 29 | 12 | 2 | 20 | 4 | 5 | 8 | 1 | 29 | 19 | 8 | 539 | 158 |



Text-figure 1.—Occurrence of otoliths from one dredge sample from the Gulf of Panama (Locality: GC-97-20, depth: 102 m, 41 otoliths) and 8 dredge samples from the Gulf of Chiriqui (GC-97-72, 41 m, 19 otoliths; GC-97-80, 64 m, 132 otoliths; GC-97-10, 65 m, 5 otoliths; GC-97-95, 65 m, 4 otoliths; GC-97-91, 65 m, 19 otoliths; CG-97-57, 65 m, 1 otolith; GC-97-97, 87 m, 67 otoliths; CG-97-79, 87 m, 22 otoliths) along the Pacific coast of Panama. Solid lines indicate the presence of the genera at the depth intervals and dashed lines indicate the nightly occurrence of mesopelagic genera near the surface. The number of genera present in any 100-m or 50-m depth interval is expressed as a percentage of the total number of taxa collected in the sample.

analyzed here come from 93 collections, including 18 collections from the Panama Canal Basin (Table 1), 58 collections from the Bocas del Toro Basin (Tables 2–4), and 17 collections from the Limon Basin (Table 5). Bulk samples were washed using 2-mm and 500-µm sieves. Otoliths from both types of collections were combined for presentation in Table 1. The data of Tables 1-5 are available at the PPP internet site http://www.fiu.edu/˜collinsl/.

## TERMINOLOGY AND TAXONOMY

Terminology and classification follow Nolf's (1985) review of otolith anatomy, morphology, variability, ontogeny and preservation. Otoliths consist of calcium carbonate, mainly aragonite, and organic matter called otoline. Otoliths are the integral, specialized hard part of the actinopterygian and sarcopterygian acousticolateralis system, situated in the membranous labyrinths. Each labyrinth is located on either side of the brain in the otic capsules of the neurocranium. Within each membranous labyrinth is a different otolith in the utriculus, sacculus and lagena. The term otolith as used in this study refers to saccular otoliths, except for catfish that are represented by utricular otoliths.

Otoliths can be identified unambiguously only when they are well preserved and common enough for comparative observations (Plate 1). A complete inventory of the faunas was not possible in this preliminary survey pending more material. In general, we have been able to make generic identifications with high confidence, but species identifications will require more detailed study and use of extensive reference collections of the otoliths of living species. Some taxa, such as *Diaphus*, present particular problems in identification (see discussions in Nolf and Steurbaut, 1987; Nolf and Capetta, 1989; Nolf and Stringer, 1992). In other cases, such as the approximately 113 Recent species of tropical western Atlantic gobiids (Richards, 1990), the taxonomy is not sufficiently resolved to allow reliable identifications because of their highly variable otolith morphologies. Furthermore, in taxa such as the sciaenids, juvenile otoliths do not exhibit diagnostic features.

## TAPHONOMY

Most otoliths probably enter the sediments through the excreta of predators (Nolf, 1985; Nolf and Brzobohaty, 1992). Large quantities of teleostean remains have been found in the stomachs of numerous large marine predators including cetaceans (Fitch and Brownell, 1968), sharks (Cortes and Gruber, 1990; Ebert *et al.*, 1992; Hazin *et al.*, 1994; Ellis *et al.*, 1996; Cortes *et al.*, 1996) and batoids (Hess, 1961; Gilliam and Sullivan, 1993; Ellis *et al.*, 1996). For example, the stomachs of 17 cetaceans, comprising seven species, contained 18,164 otoliths of fishes, of which more than 89 percent were Myctophidae (lanternfish). However, observations of the occurrence of otoliths in Recent sediments are limited. Most otoliths along the east coast of North America occur on the continental slope (400–2,000 m), whereas otoliths are much less abundant on the continental shelf (<100 m), possibly because fluctuations in sea level greatly reduce the time

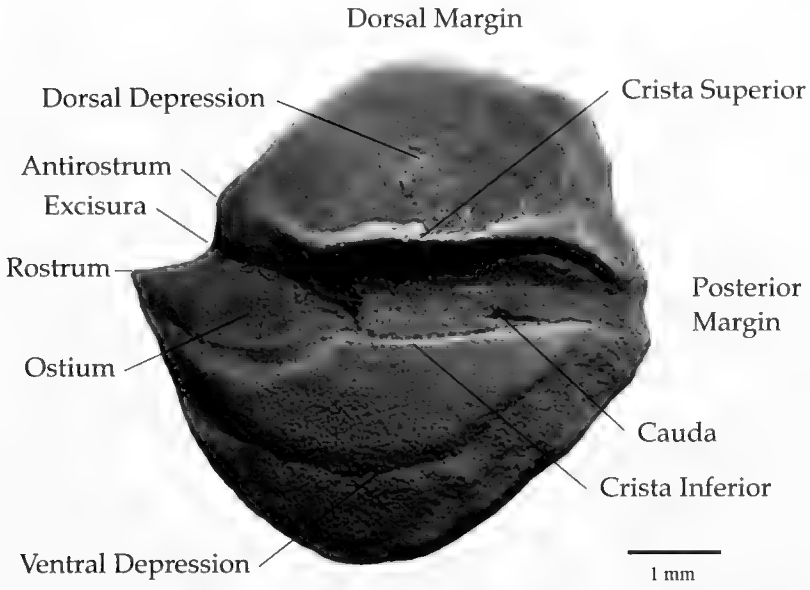


PLATE 1

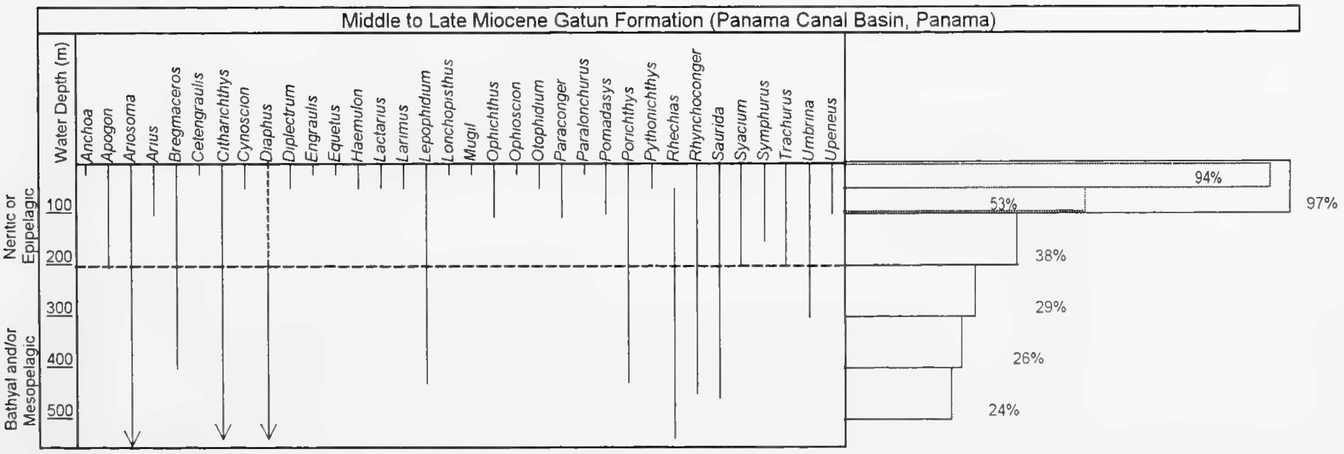
Principal morphological features of the mesial surface of a right otolith (*Epigonus denticulatus*, Dieuzeide, 1950), PPP 5057, from the Early Pliocene Cubagua Formation, Venezuela.

for otoliths to accumulate at shallower depths (Elder *et al.*, 1996).

These problems raise questions about how well the occurrence of otoliths in sediments reflects their distributions in life. To begin to address this question, we examined otoliths from nine sediment samples obtained by dredging in depths of 41–102 m in the Gulfs of Panama and Chiriqui along the Pacific coast of Panama (Text-fig. 1). All of the genera obtained have representatives among the fossils collected from the Limon, Bocas del Toro, and Panama Canal basins. Otoliths were identified based on examination of specimens of living species from the area. Data on depth of occurrence and life habits of living fishes (Allen and Robertson, 1994) were compared to the depth of collection and bottom conditions at the sites of collection of the dredge samples (H. Fortunato, oral communication, 1998).

## ESTIMATES OF PALEOBATHYMETRY

We used all the samples from the same formation to make one estimate of paleobathymetry, using the method of Nolf and Brzobohaty (1992). The method is based on the assumption that the taxa encountered



Text-figure 2.—Present-day bathymetric ranges of taxa represented in the Gatun Formation. Solid and dashed lines drawn as in Text-figure 1.

lived together in the same environment represented by the sedimentary facies sampled. The assumption appears reasonable, because of the general lithologic uniformity within the formations sampled and the agreement with estimates of paleobathymetries based on benthic foraminifera (Collins, 1993; Collins *et al.*, 1995, 1996, this volume). All the identifiable otoliths from the samples were identified to genus and depth ranges were assigned to each taxon based on the known depths of living counterparts. We did not attempt to estimate water depths for assemblages of less than 15–20 species from any formation.

The number of genera in each 100-m depth interval was converted to the percentage of the total genera in the formation. Occasionally it was possible to subdivide the first 100-m interval into two based on the occurrence of common, shallow-water taxa. The depth profile of the formation is thus characterized by varying percentages of taxa per depth interval. These percentages usually peak at a single 100-m depth interval that is then taken as the most likely paleodepth of the formation. However, sometimes two peaks may occur, possibly due to reworking of sediments. In such cases, an estimation of paleodepth is unreliable.

## THE NEOGENE FAUNA

We obtained 7,770 otoliths distributed among 81 taxa, 70 identified to genera, or about ten percent of the 773 western central Atlantic genera alive today (Richards, 1990). The comparatively low fossil diversity is due to several factors, including: (1) small numbers of samples, (2) differential preservation among facies, (3) numerous broken or abraded specimens, (4) presence of juvenile forms without diagnostic features, and (5) abundance of families whose otoliths are undescribed or poorly known. The first three problems can be readily addressed by more extensive sampling, but the rest require much more work on the otolith morphology of Recent species.

The fauna has strong similarities to the Neogene teleostean faunas of the Dominican Republic (Nolf and Stringer, 1992), Trinidad (Nolf, 1976), Jamaica (Stringer, 1998) and Venezuela (Nolf and Aguilera, 1998). The most common taxa are ariids, clupeids, myctophids, gerreids, pomadasids, sciaenids, gobiids and ophiids. Most are neritic with a few mesopelagic or demersal taxa from the upper slope.

The presence of *Lactarius* is of special interest because the one Recent species of the genus, *L. lactarius* Schneider, is known only from coastal waters of southern Asia (Nolf and Bajpai, 1992). Fossil lactariids are known from the Middle Eocene of Barbados, the Paleogene of the Gulf of Mexico and Europe, the Aquitaine Basin of France, and the Miocene of Portugal and the Dominican Republic (Steurbaut, 1984; Nolf and Stringer, 1992). *Lactarius* appears to be a Tethyan relict that survived in the southwest Caribbean until at least the Late Pliocene (Rio Banano Formation, Table 5). The Indo-Pacific genus *Plotosus* is another Tethyan relic that occurs in the Neogene of the Dominican Republic (Nolf and Stringer, 1992) and Panama (Table 3).

## TEST OF THE PALEOBATYHMETRY METHOD FOR RECENT FAUNAS

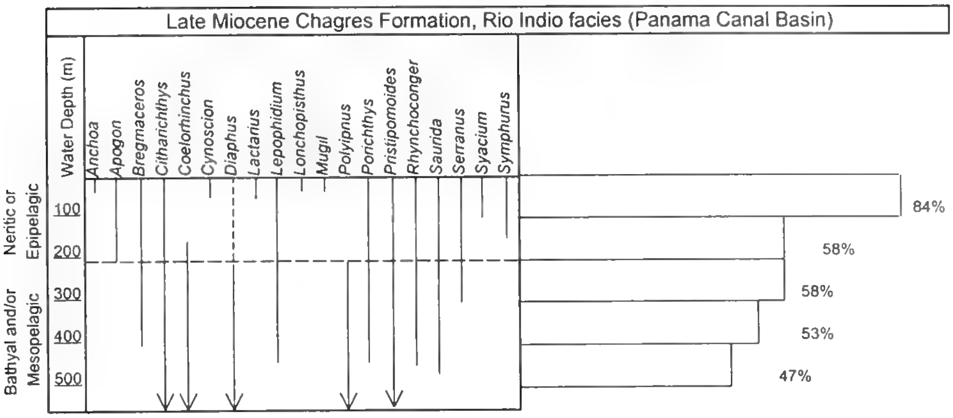
Nine dredge samples that were collected between 41-102 m from the Pacific coast of Panama were analyzed. They yielded 310 identifiable otoliths of 33 genera (Text-fig. 1). All but five (85%) live exclusively in depths of 100 m or less, over sandy or muddy bottoms, and 91% occur in depths of 0–50 m (Allen and Robertson, 1994). Most are benthic (*e.g.*, gilbert flounder *Citharichthys gilberti*, conger eel *Paraconger californiensis*, spinesnout brotula *Lepophidium prorates*, longtailed jawfish *Lonchopisthus sinuscalifornicus*) or live in the lower part of the water column above the bottom (*e.g.*, croaker *Micropogonias ectenes*, serrated grunt *Conodon serrifer*, banded serrano *Serranus psittacinus*). Five of the taxa are bathyal or mesopelagic. However, only two of these (*Neobythites stelliferoides* and *Coelorhincus* aff. *C. scaphopsis*) are restricted to such depths and therefore were probably transported upwards by predators. Thus, the otolith fauna matches very well the life habits of the species collected.

## ESTIMATES OF PALEOBATHYMETRY OF NEOGENE FAUNAS

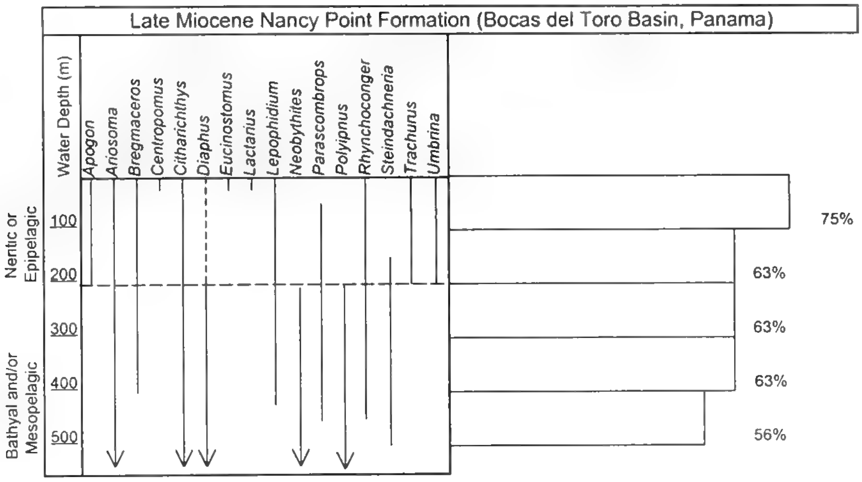
### PANAMA CANAL BASIN

#### *Gatun Formation (12 collections, 874 otoliths)*

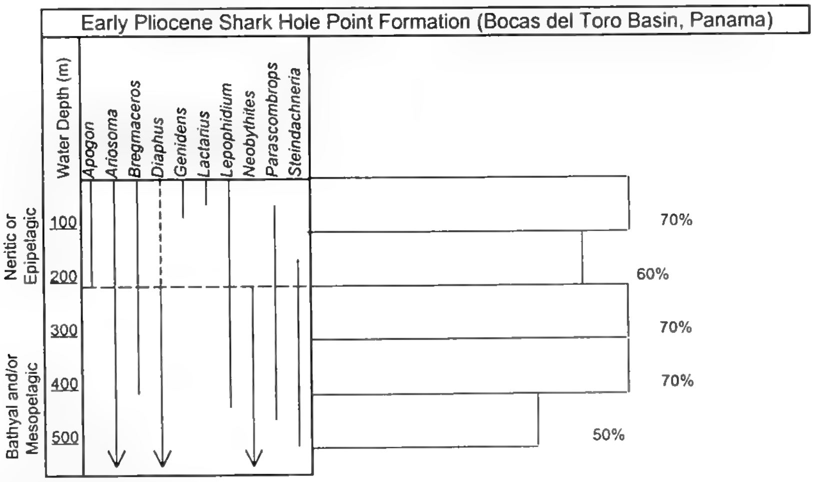
The 34 taxa from the Middle to Late Miocene Gatun Formation are the second most diverse assemblage from this preliminary survey (Text-fig. 2; Table 1). The fauna includes several neritic sciaenids such as the jacknifefish, *Equetus*, the weakfish, *Cynoscion*, the shorthead drum, *Larimus*, the croaker, *Ophioscion*, and the barbel drum, cf. *Ctenosciaena*. Also present is the Tethyan relic false trevallies fish, *Lactarius*. These taxa, together with the anchovy, *Anchoa*, the anchoveta, *Cetengraulis*, the anchovy, *Engraulis*, the jawfish, *Lonchopisthus*, and the mullet, *Mugil*, are all mainly shallow-water fishes that live at depths less than 25 m (Text-fig. 2). Living representatives of 94% of the fauna occur in depths less than 50 m, whereas only one third range into bathyal depths. Our paleobathymetric estimate of 0–50 m is strongly supported by assemblages of benthic foraminifera that suggest depths of 20–40 m (Collins *et al.*, 1996).



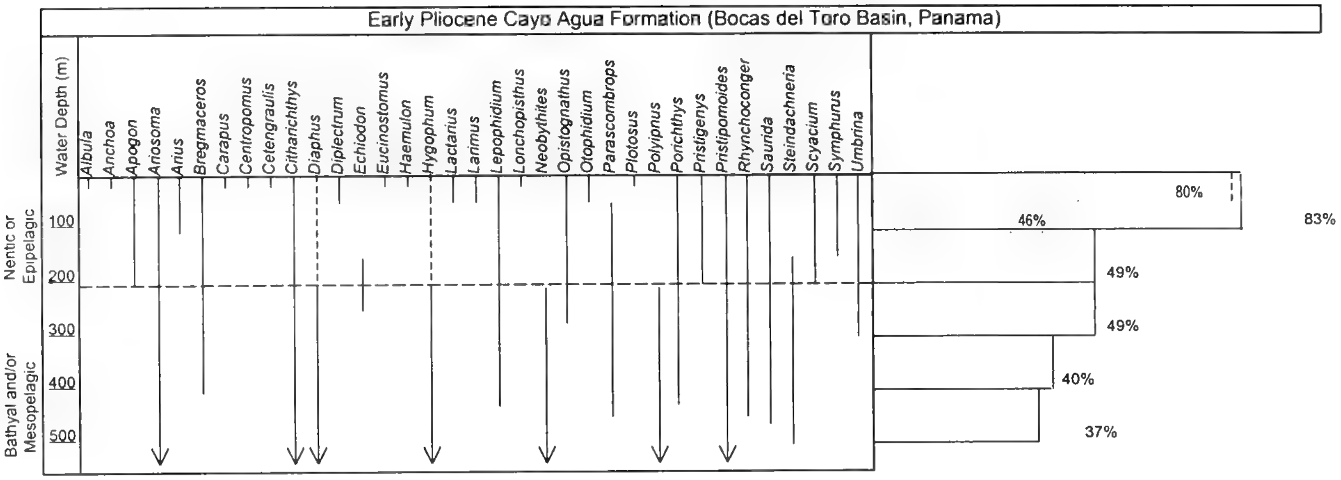
Text-figure 3.—Present-day bathymetric ranges of taxa represented in the Chagres Formation. Solid and dashed lines as in Text-figure 1.



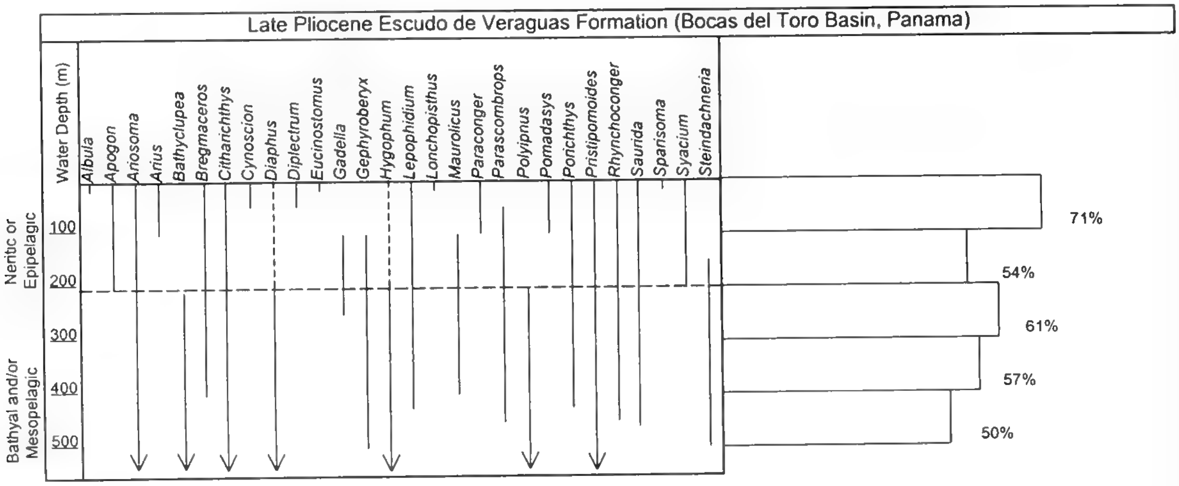
Text-figure 4.—Present-day bathymetric ranges of taxa represented in the Nancy Point Formation. Solid and dashed lines drawn as in Text-figure 1.



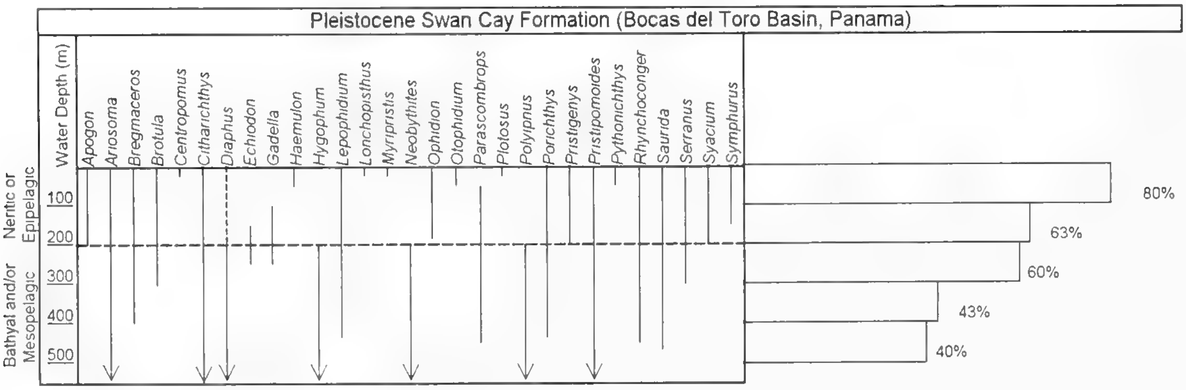
Text-figure 5.—Present-day bathymetric ranges of taxa represented in the Shark Hole Point Formation. Solid and dashed lines drawn as in Text-figure 1.



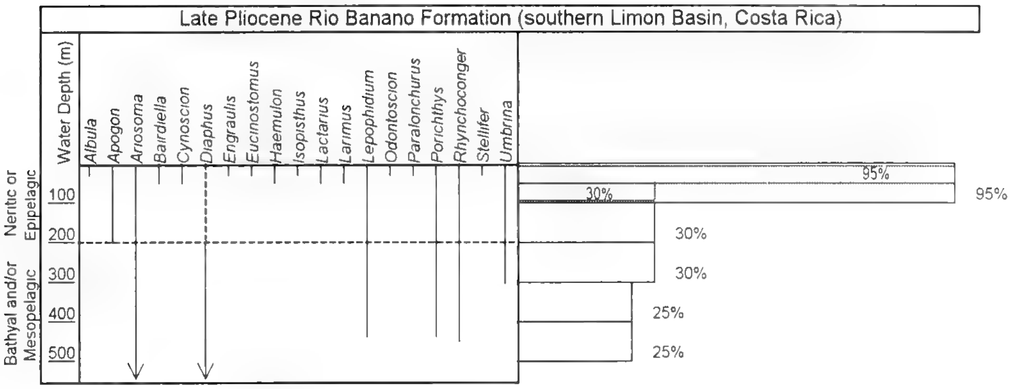
Text-figure 6.—Present-day bathymetric ranges of taxa represented in the Cayo Agua Formation. Solid and dashed lines drawn as in Text-figure 1.



Text-figure 7.—Present-day bathymetric ranges of taxa represented in the Escudo de Veraguas Formation. Solid and dashed lines drawn as in Text-figure 1.



Text-figure 8.—Present-day bathymetric ranges of taxa represented in the Swan Cay Formation. Solid and dashed lines drawn as in Text-figure 1.



Text-figure 9.—Present-day bathymetric ranges of taxa represented in the Rio Banano Formation. Solid and dashed lines drawn as in Text-figure 1.

### *Chagres Formation (6 collections, 1,908 otoliths)*

The 20 taxa from the Rio Indio facies of the Late Miocene Chagres Formation include a mixture of neritic and bathyal forms, but 80% have living representatives that inhabit depths less than 100 m versus 45–60% for deeper water (Text-fig. 3; Table 1). The suggested paleobathymetric range of 0 to 100 m compares favorably with that based on benthic foraminifera (Collins *et al.,* 1996).

## BOCAS DEL TORO BASIN

### *Nancy Point Formation (13 collections, 178 otoliths)*

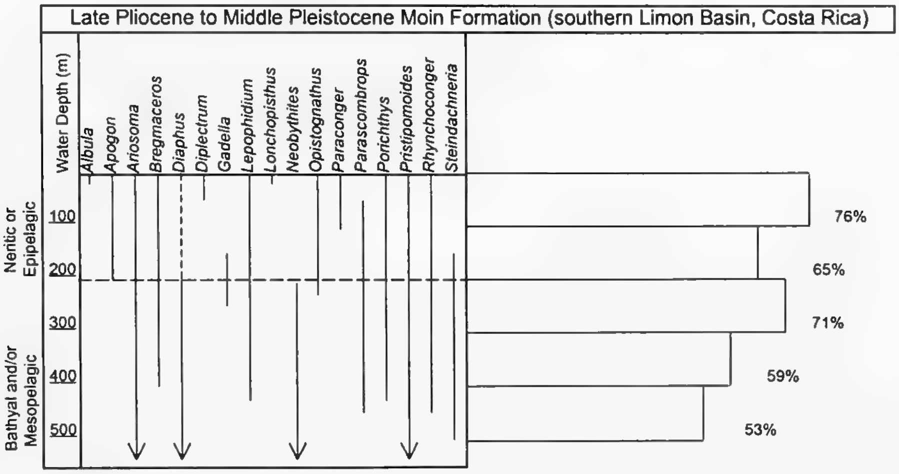
The Late Miocene Nancy Point Formation yielded only 12 taxa, with no clear indication of paleobathymetry (Text-fig. 4; Table 2). The estimate of 300–500 m based on foraminifera (Collins, 1993) is consistent with the limited information on otoliths.

### *Shark Hole Point Formation (8 collections, 51 otoliths)*

The Early Pliocene Shark Hole Point Formation contained only nine taxa of mixed environmental affinities (Text-fig. 5; Table 2). The mesopelagic lanternfish, *Diaphus,* the codletsfish, *Bregmaceros,* the cusk eel, *Lepophidium,* and *Steindachneria* range widely in depth. Likewise, the conger eel, *Ariosoma,* includes several neritic Recent species, but the Caribbean *A. selenops* inhabits the continental slope down to 550 m (Nolf and Brzobohaty, 1992). The only exclusively shallow-water fishes are the estuarine catfish, *Genidens,* and *Lactarius.* The estimate of 100–200 m based on benthic foraminifera (Collins *et al.,* 1995) is consistent with the limited data for otoliths.

### *Cayo Agua Formation (13 collections, 634 otoliths)*

The 37 taxa from the Early to Middle Pliocene Cayo Agua Formation comprise the most diverse teleostean



Text-figure 10.—Present-day bathymetric ranges of taxa represented in the Moin Formation. Solid and dashed lines drawn as in Text-figure 1.

assemblage obtained in this preliminary survey (Text-fig. 6; Table 3). The fauna contains diverse estuarine taxa such as the bonefish, *Albula,* the snook, *Centropomus,* the mojarra, *Eucinostomus,* and *Larimus,* all suggesting a water depth of less than 50 m. Also present is the catfish *Plotosus,* which is another Paleogene, western Tethyan relict that lives today in principally neritic, estuarine, or even fresh waters of the Indo-Pacific and Australian realms (Nolf and Stringer, 1992). Taxa whose living representatives occur in depths less than 50 m comprise 84% of the fauna, whereas those found in bathyal depths are less than half to one third the taxa. Our estimate of 0–100 m compares favorably with that of 20–80 m based on benthic foraminifera (Collins, 1993).

### *Escudo de Veraguas Formation (20 collections, 920 otoliths)*

The 27 taxa from the Late Pliocene Escudo de Veraguas Formation comprise a mixed neritic and mesopelagic ichthyofauna with no obvious peak (Text-fig. 7; Table 4). The general decline in diversity of taxa whose living representatives are known from deeper waters suggests a paleobathymetry of somewhere between 0–300 m. This is compatible with the estimate of 100–150 m based upon benthic foraminifera (Collins *et al.,* 1995).

### *Swan Cay Formation (4 collections, 2,289 otoliths)*

The Early Pleistocene Swan Cay Formation contains an ecologically diverse assemblage of 30 taxa of predominantly shallow-water affinities (Text-fig. 8; Table 3). The estimated depth of 0–100 m is similar to that of 80–120 m based on benthic foraminifera (Collins in Jackson *et al.,* this volume).

## LIMON BASIN

### *Uscari Formation (3 collections, 8 otoliths)*

The Early to Middle Miocene Uscari Formation (uppermost part) produced the lowest abundance and diversity, yielding only eight otoliths of the mesopelagic lanternfish, *Diaphus,* that exhibits a wide depth range. The locality sampled (Appendix B, this volume, Section 27) is about 6.0–5.0 Ma (Coates *et al.,* 1992) with a depositional depth of 300–500 m, based on benthic foraminifera (Collins *et al.,* 1995).

### *Rio Banano Formation (7 collections, 77 otoliths)*

Living representatives of most of the 19 taxa found in the Late Pliocene Rio Banano Formation inhabit depths less than 50 m (Text-fig. 9; Table 5). The sciaenid, *Stellifer,* lives primarily near the shoreline. The croaker, *Umbrina, Ariosoma, Lepophidium,* the Atlantic midshipman, *Porichthys,* and the conger fish, *Rhynchoconger,* range today from shallow waters to depths of 300 to 500 m. The only oceanic taxon is *Diaphus,* which today occurs mainly between 200–1,000 m. However, individuals migrate each night to the surface where they may be eaten by epipelagic predators which could excrete *Diaphus* otoliths in the neritic environment (Nolf, 1985; Nolf and Brzobohaty, 1992). Ninety-five percent of the taxa live today in depths of 0–50 m, which agrees very well with the estimate of 20–40 m based on benthic foraminifera (Collins *et al.,* 1995).

### *Moin Formation (7 collections, 762 otoliths)*

Half of the 17 taxa from the Late Pliocene to earliest Pleistocene Lomas del Mar Member of the Moin Formation range across neritic to bathyal depths with no clear peak in diversity (Text-fig. 10; Table 5). Only *Neobythites* and *Diaphus* are oceanic. The estimated paleobathymetry of 50–100 m based on benthic foraminifera (Collins *et al.,* 1995) and 40-73 m based on ahermatypic corals (Cairns, this volume) are consistent with the otoliths but appear somewhat deep for the abundant and diverse reef coral assemblage that occurs in place in the same deposit (Coates *et al.,* 1992; Budd *et al.,* this volume).

## CONCLUSIONS

1. Preliminary collections of a Neogene ichthyofauna from three Caribbean sedimentary basins of Panama and Costa Rica yielded identifiable otoliths of 70 genera. Most of these are alive today, which permits estimates of paleobathymetry based on the otolith assemblages.
2. Estimates of paleobathymetry based on diverse assemblages of otoliths were in good agreement with those based upon benthic foraminifera.
3. Reworking of otoliths by physical or biological transport apparently does not badly obscure original patterns of depth distribution.
4. The great abundance and distribution of Neogene otoliths from these sediments constitute a rich resource for future investigations of paleoecology and systematics.

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# CHAPTER 12

## A DATA MODEL FOR THE PANAMA PALEONTOLOGY PROJECT

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### INTRODUCTION

The goal of the Panama Paleontology Project (PPP) is to describe the geological and biological events leading up to the complete emergence, approximately 3 million years ago, of the land bridge connecting North and South America. Field work in support of the project has required numerous collecting trips to remote areas in Panama, Costa Rica, Nicaragua, Ecuador and Venezuela since 1986. These trips have resulted in the collection of almost 5,000 samples of fossil invertebrates. The samples have in turn been divided and shipped to over 30 active scientists in 8 countries. There is a substantial interdependence among the collaborators on the results obtained by the others. It is imperative to track accurately the location and status of preparation of the samples; to integrate age analyses, stratigraphy, section measurements, and paleoenvironmental interpretations; and to distribute this information to other collaborators.

### WHAT IS A DATA MODEL AND WHY MAKE ONE?

A data model is an abstract representation of the information used by an organization. The model is expressed as a list of entities and their interactions that the members of the organization deal with. Examples of entities for the PPP are either distinct objects such as SAMPLEs; places, such as collection SITEs; pieces of information such as AGE DETERMINATIONs; or abstract ideas, such as an assignment of a SITE to a CORRELATED SITE. (Note that the names of entities are in capital letters.) Each of these entities has a list of attributes that describe the entity. For example, the entity SAMPLE has Collector ID and Sample Collection Date among its attributes. (Names of attributes have the first letter of each major word capitalized). Individual instances (or occurrences) of an entity are related to individual instances of other entities. These are called relationships and their verbal descriptions form part of the model as well.

One reason for making a data model is to determine how best to arrange the data into tables, where each table represents a particular entity as described above. The overriding goal is to reduce redundancy in the database. It is a common mistake to define entities too broadly. For example, suppose that instead of defining a SAMPLE entity and a SUBSAMPLE entity separately it were decided to combine them into one table. Then, information, such as Sample Collection Date, that relates only to the SAMPLE as a whole, would have to be repeated each time a row is added for another SUBSAMPLE extracted from a single SAMPLE. This opens the possibility for a type of error where one SAMPLE could have two different collection dates, one for each SUBSAMPLE extracted from it. Subsequent queries based on Sample Collection Date would then be in error. There are other more subtle ways that duplication of data can occur, and the process of making a data model eliminates them. Once the data are properly arranged into tables, then entering data, finding and correcting errors, expanding the scope of the database if required, and extracting data is all much easier.

There is another equally important reason for making a data model. The model, and in particular the graphical representation of the model, provides a means of explaining the working of the database and the project itself to the users. The model is supposed to represent real-life things, easily identified by people who have to work with the data. By arranging the data in an organized way and explicitly defining all of the terms and concepts used by the organization, the model provides a common means of communication between the users, who are well versed in the complexities of the organization, and the people designing the database, who may know less about the organization but more about relational database technology.

Finally, the process of producing a logical data model puts the data in the format required by a relational database. When a relational database is used, queries on the data may be executed using Structured Query Language (SQL), a powerful query language developed specifically for this type of database. Many commercial databases support this language, so that SQL commands written for one particular database program may be used unaltered in another.

## CONVENTIONS USED IN THE PPP DATA MODEL

The data model of the PPP is described both graphically (Text-figs. 1–2) and verbally (Definitions of Entities and Attributes below) (Teorey, 1990; Fleming and von Halle, 1989). Each entity in Text-figure 1 is represented by a box. Above each of the boxes is the name of the entity, such as SITE or STRATIGRAPHIC UNIT. Inside each box are a list of attributes of that entity.

When a data model is transformed into a working database, the entities become tables, and the attributes become columns (also called fields) in those tables. An individual instance of an entity is represented by the information in a single row (also called a record) of its table. It may be easier in the following discussion for the reader used to working with a database to think in terms of tables, columns, and rows rather than entities, attributes, and instances.

At the top of each list of attributes in Text-figure 1, above the line in the box and in bold letters, are one to four attributes with special significance. These attributes, taken together, uniquely identify an individual instance of the entity and are called primary keys. There can also be other attributes that uniquely identify instances of an entity and they are called alternate keys. For example, in the entity SAMPLE, the combination of Collector ID and Field Code uniquely identifies any one sample. A person wanting to connect his own personal list of samples with the data in the PPP Database might use these like a primary key, but all references from within the PPP database will be to the Project Sample Number, which is therefore considered the primary key.

Bullets in each box mark foreign keys. A foreign key is an attribute that is a primary key for some other entity. They do not have to be unique (except in the entity for which it is a primary key), and often are not. For example, in the SITE entity, the attribute Stratigraphic Unit ID is a foreign key because it is a primary key in the STRATIGRAPHIC UNIT entity. In this case, the same Stratigraphic Unit ID may appear many times as an attribute of SITE but will correspond to only one STRATIGRAPHIC UNIT and hence appear only once in the STRATIGRAPHIC UNIT entity. When two attributes together make up a foreign key, their bullets are tied together with a short line.

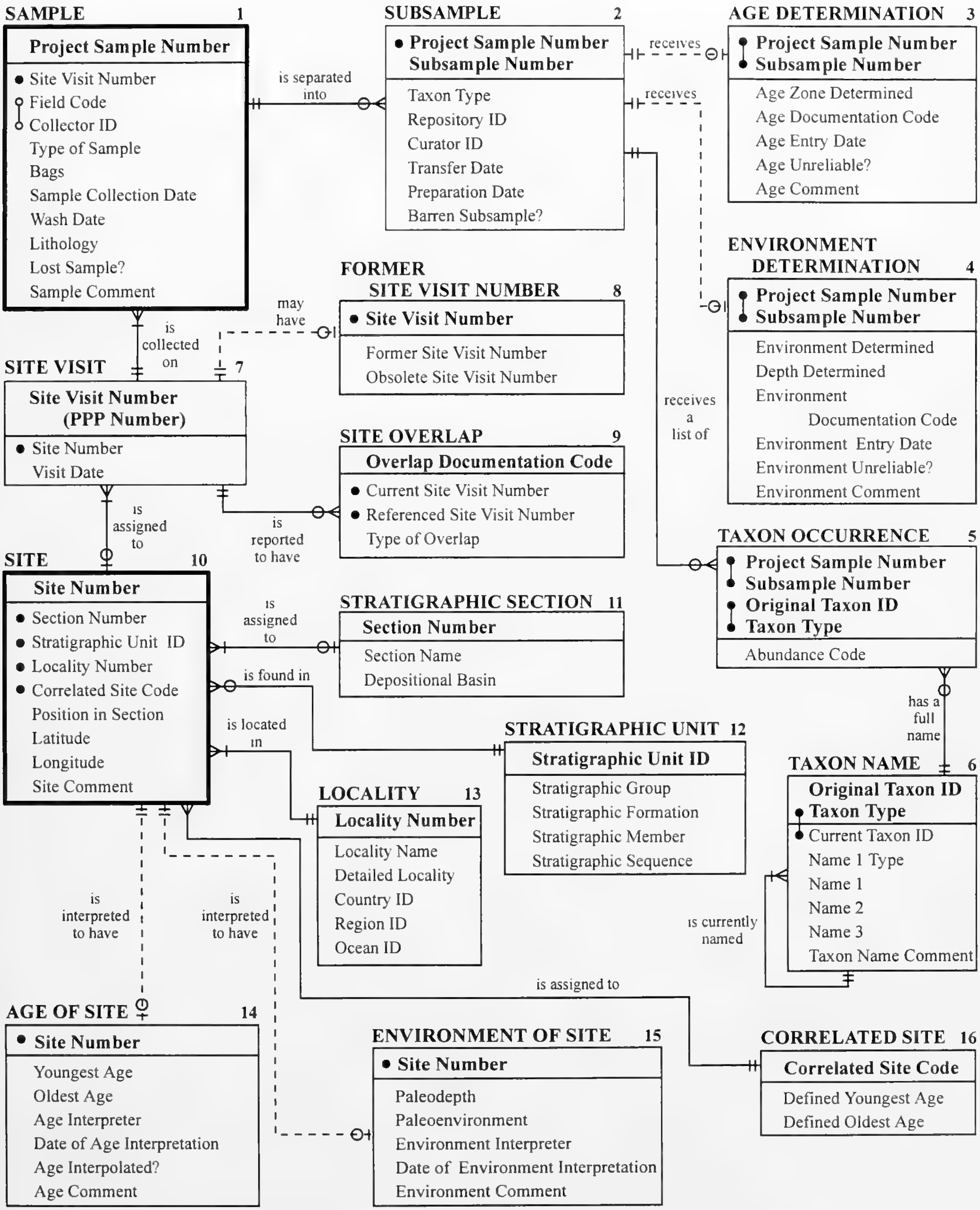
Between the boxes representing entities are lines that indicate how individual instances of one entity are related to individual instances of another. The lines have hash marks, circles, and crow's feet on them that describe how many of one instance is related to how many of the other. A verbal description of the relationship is also placed near each line. For example, a SITE is found in a STRATIGRAPHIC UNIT, hence the description of the relationship: *is found in.* A SITE is found in one and only one STRATIGRAPHIC UNIT. The symbols on the line between the boxes represent this aspect of the relationship with two hash marks. The hash mark nearest the STRATIGRAPHIC UNIT box indicates that the maximum number is 1, and the hash mark slightly further away indicates that the minimum number is also one. The symbol indicating the maximum is always immediately adjacent to the box, and the one indicating the minimum is always slightly further away.

The relationship may also be described from the STRATIGRAPHIC UNIT side of the relationship. A STRATIGRAPHIC UNIT can contain many different SITEs. It is also possible that a STRATIGRAPHIC UNIT has not yet been sampled, and hence contains zero SITEs. These aspects of the relationship are indicated by a crow's foot, indicating that 2 or more SITEs may be in a STRATIGRAPHIC UNIT or by a 0, indicating that no sites are found there. Note that the words describing the relationship, "is found in" and "contains", change with direction. Only the description for the direction of left to right or top to bottom have been placed in Text-figure 1, for brevity.

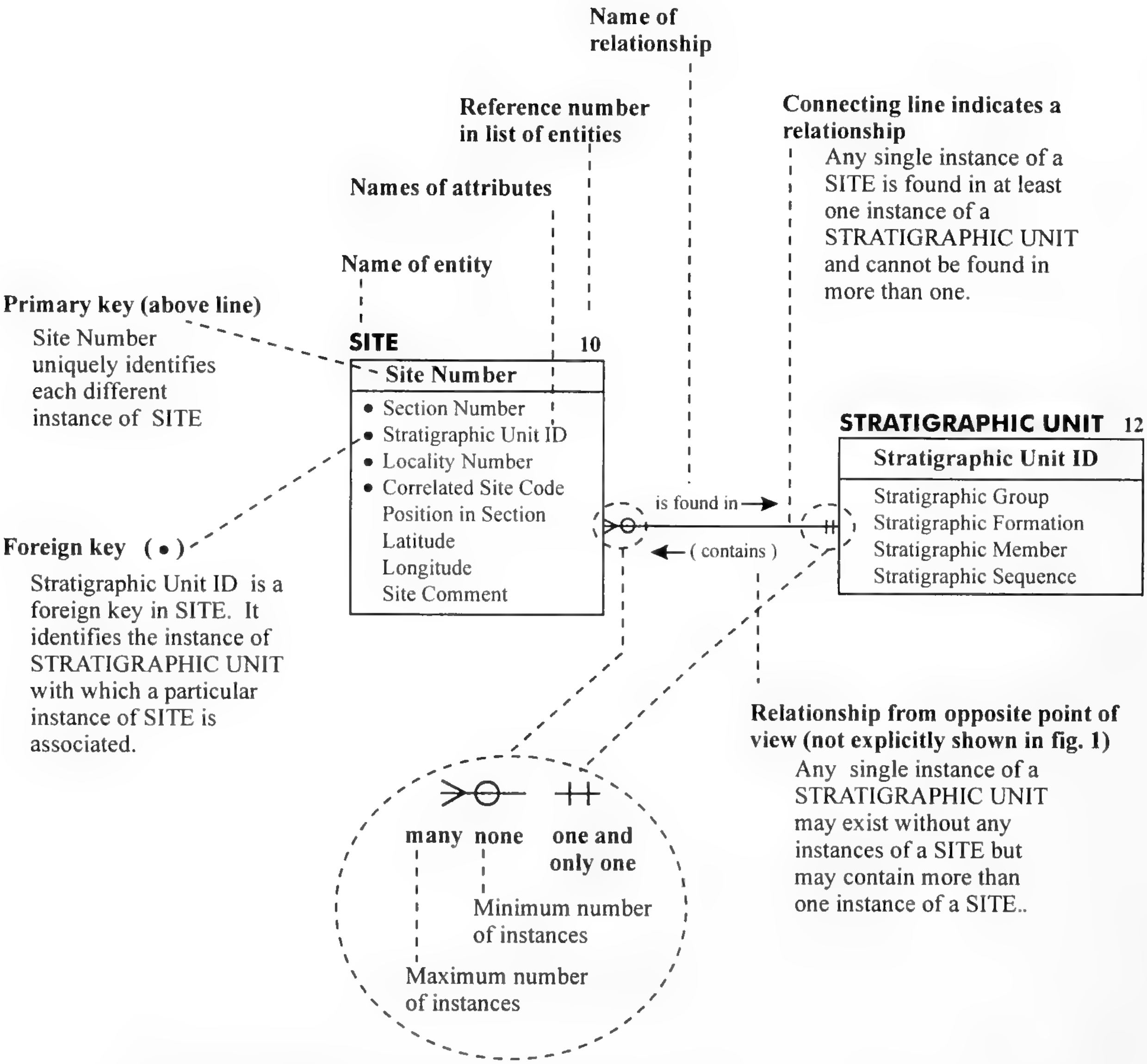
A special kind of entity is a subtype, which represents a subset of another entity called the supertype. A subtype actually represents the same entity as the supertype, and hence has the same primary key, but includes some additional information. AGE DETERMINATION is a subtype of SUBSAMPLE and includes information about the age of a sample returned by the investigator. This information is placed into a separate entity because not all SUBSAMPLEs have an AGE DETERMINATION, and including the attributes for the age in SUBSAMPLE would otherwise result in the presence of many null values. To indicate that an entity is a subtype, the line indicating the relationship is dashed.

## BRIEF SUMMARY OF THE PPP DATA MODEL

The following section summarizes the entities in Text-figure 1 and the relationships connecting them. A complete definition of each entity and its attributes is found in the last section. The two main entities in the PPP database are SAMPLE and SITE, shown with a thick outline in Text-figure 1. SAMPLEs are the actual



Text-figure 1.—Entity-relationship diagram, the Data Model for the Panama Paleontology Project.



**Connecting line indicates a relationship**

Any single instance of a SITE is found in at least one instance of a STRATIGRAPHIC UNIT and cannot be found in more than one.

**Primary key (above line)**

Site Number uniquely identifies each different instance of SITE

**Foreign key (•)**

Stratigraphic Unit ID is a foreign key in SITE. It identifies the instance of STRATIGRAPHIC UNIT with which a particular instance of SITE is associated.

**Relationship from opposite point of view (not explicitly shown in fig. 1)**

Any single instance of a STRATIGRAPHIC UNIT may exist without any instances of a SITE but may contain more than one instance of a SITE..

\- - - - - - - **Dashed relationship line**

Indicates that one entity is a subtype of the other. This means it has the same primary key and the relationship is one to one or one to none.

I **Multiple primary keys, Foreign key symbols tied together**

Sometimes two or more attributes are needed to uniquely define an entity. This is indicated for primary keys by including two or more entities above the line in the box. For foreign keys, this is indicated by tying together the symbols.

○ **Alternate key**

An attribute that uniquely identifies an entity, but is not directly used to access the data in the table.

Text-figure 2.—Key to Data Model of Text-figure 1.

objects collected in the field, and SITEs are the places where the SAMPLEs were collected.

Each SAMPLE is separated into one or more SUBSAMPLEs which are sent to participants in the project for analysis. A SUBSAMPLE consists of a selection of fossils of a particular type, corals or foraminifera, for example. A participant may return an AGE DETERMINATION or an ENVIRONMENT DETERMINATION based on the fossils found in that particular sample. Or, the participant may return a list of TAXON OCCURRENCEs, i.e. a species list, for the SAMPLE. This list will be stored as Original Taxon IDs which are unique for each Taxon Type and which will have full scientific TAXON NAMEs, or an informal description of the fossil.

A SAMPLE is collected on a SITE VISIT and all SAMPLES collected from exactly the same place on the same trip receive the same Site Visit Number (also called the PPP_number). Early in the project, SAMPLEs were assigned different identifiers and thus may have a FORMER SITE VISIT NUMBER.

In the field, collectors may record that a SAMPLE collected on a particular SITE VISIT is closely associated with another SITE VISIT. The SAMPLE may have been collected at nearly the same SITE used in a previous trip, it may span or be included in the same SITE, it may be adjacent to the same SITE, or it may be collected at exactly the same site as another SAMPLE. These observations are recorded as a SITE OVERLAP.

A SITE is a location on an outcrop from which one or more SAMPLEs have been taken, perhaps on different collecting trips. Hence, repeat visits to a SITE, say three visits in a five year period, will result in three different SITE VISITs, all of which will receive the same Site Number. This code is, by convention, the same as the first Site Visit Number assigned.

Each SITE has a LOCALITY, which is a place that can be found on a map. Several SITEs may have the same LOCALITY. SITEs will also be assigned to a STRATIGRAPHIC SECTION, which is a drawn figure showing the local stratigraphy and the relationship of all the sites within a Depositional Basin. SITEs also belong to a particular STRATIGRAPHIC UNIT.

From AGE DETERMINATIONs and ENVIRONMENT DETERMINATIONs returned about SAMPLEs collected at each SITE, and at nearby SITEs, it is possible to interpret an AGE OF SITE and ENVIRONMENT OF SITE for each SITE. In some cases the determination is direct, in other cases it is interpolated from directly dated SITEs above or below the SITE. In either case, a responsible scientist, the Age Interpreter or Environment Interpreter, is needed to interpret possibly conflicting reports for AGE DETERMINATIONs or ENVIRONMENT DETERMINATIONs for relevant SAMPLEs.

Many SITEs will overlap in upper and lower time boundaries. For example a series of micro samples may be taken through a section where macro fossils were collected. In order to provide macro fossil workers with a set of named, non-overlapping SITEs to use in their work, SITEs are grouped into CORRELATED SITES by Coates, the Chief Stratigrapher. These span a broader geographical area and have a coarser division of geological time.

## IMPLEMENTING THE MODEL WITH VISUAL FOXPRO

This data model does not assume the use of any particular commercial database program for its implementation. Any program capable of working with relational tables (which is what the entities represent) could be used. The PPP uses Microsoft Visual Foxpro 6.0 (VFP) for the implementation because of its well developed programming environment which makes setting up the database, entering data, writing reports, and maintaining the program relatively easy. However, just because VFP is used to enter and maintain the data does not mean that executing queries on the database requires the same program. In fact, as mentioned above, any database program capable of executing Structured Query Language (SQL) commands could be used.

In implementing the data model with VFP, each entity becomes a separate table, and the attributes become fields, or columns, in each table. For entering data and enforcing the rules governing the relationships, commands specific to VFP, not SQL, are used. An example of one such rule is: a particular SUBSAMPLE cannot exist without a SAMPLE to which it belongs. VFP has a data dictionary which makes the enforcement of most rules, including this one, automatic. Investigators not using copies of the database for SQL queries, receive reports in the form of printed tables or made-to-order VFP tables which they can access on their own computer.

## USING STRUCTURED QUERY LANGUAGE TO EXTRACT INFORMATION

Structured Query Language (SQL) was developed specifically for working with relational databases. One of the commands, the SELECT command, is particularly adept at combining information from many different tables and placing it in a single report or another table. For example, with just one (rather complex) SQL command, a list could be prepared of all samples collected by a particular collector (found in SAMPLE), and in a particular Stratigraphic Formation (found in

STRATIGRAPHIC UNIT) along with the interpreted Youngest Age and Oldest Age (found in AGE OF SITE) for the SITE to which it belongs. This information could be presented on the screen as if it were in a single table, or placed in a separate table and viewed on a remote computer where it could be imported into a favorite spreadsheet, or it could be put into a printed report. VFP, as well as earlier versions of Foxpro and other commercial databases, support the SQL SELECT command. Scientists learning SQL will be able to quickly extract specialized information beyond the prepared reports distributed to them.

## DEFINITIONS OF ENTITIES AND ATTRIBUTES

The following contains precise descriptions of each entity and its attributes. The entity names are in upper case letters and are preceded by a number corresponding to the numbers on the boxes in Text-figure 1. Entity names are followed by a description and then a short list of one or more attributes which provides the primary key for the entity. Then the attributes, starting with the primary key, are listed after each entity name, along with their descriptions. The domain is the set of possible values an attribute may have. The statement "not null" indicates that the field must have some value other than blank or zero, *e.g.*, a default value. To refer to an entity's attribute, the format ENTITY.Attribute (*e.g.*, SAMPLE.Field Code) is used.

### 1 SAMPLE

A collection of fossils, rocks, or sediment taken from a single SITE (see definition of SITE below). It can include both loose fossils, fossils in matrix, and drilled cores for paleomagnetic analysis. The entire SAMPLE must be collected on a single trip and only one person is identified as the collector.

*Primary key:* Project sample number
*Foreign key:* Site Visit Number
*Alternate key:* Field Code + Collector ID

**1.1 Project sample number:** The number identifying each SAMPLE collected by a PPP participant. Numbers are assigned by the data manager in the order in which they are inventoried at the Smithsonian Tropical Research Institute (STRI).

*Domain:* PSN000001-PSN999999. Not null.

**1.2 Site Visit Number:** Tells on which SITE VISIT the SAMPLE was collected.

*Domain:* Same as SITE VISIT.Site Visit Number. Not null.

**1.3 Field Code:** The private sample code used by each collector and recorded in his field notes. The codes are unique for each collector and in many cases have been used for many years preceding this project. The combination of Field Code and Collector ID is unique and serves as an alternate key to SAMPLE. This key is not used within the database, but will be useful for investigators needing to combine PPP data with their own records. An assistant taking SAMPLEs assigns his supervisor's code.

*Domain:* Numbers, characters, spaces and "-" up to 12 characters long. Not null.

**1.4 Collector ID:** The initials of the person collecting the SAMPLE. The initials are unique for each person in the project and in case of conflict are assigned by the data manager. SAMPLEs taken by an assistant are assigned the supervisor's initials. Together with Field Code, uniquely identifies the SAMPLE collected.
*Domain:* Same as SUBSAMPLE.Curator ID. Not null.

**1.5 Type of Sample:** The type of SAMPLE collected. Types are:

| | |
|---|---|
| micro | Small bag of sediment used for microfossils |
| strib | Large bulk SAMPLE kept at STRI for processing |
| basb | Large bulk SAMPLE sent to the Naturhistorisches Museum, Basel, for processing |
| spec | Specimens collected individually from sediments in place |
| float | Specimens collected individually from sediments not in place |
| litho | Lithified rock sample, *e.g.*, basalt, coquina |
| pmag | Drilled core for paleomagnetic analysis |
| unknw | Type unknown to the data manager |

*Domain:* The above codes, all lower case. Not null.

**1.6 Bags:** SAMPLEs are usually put into one or more cloth bags in the field.

*Domain:* Integers 1 to 99. Default is 1.

**1.7 Sample Collection Date:** The date the SAMPLE was collected. Sometimes, collections are made at a SITE over a period of several days, so different SAMPLEs may be collected on different dates from the same SITE VISIT. Hence Sample Collection Date is an attribute of SAMPLE, not SITE VISIT.

*Domain:* All calendar days since the beginning of the project. Not null.

**1.8 Wash Date:** The date that either: 1) a specimen or float SAMPLE was washed, glued, sorted, and boxed or 2) the date that a micro, basb, or strib SAMPLE was cooked and washed. (The date of a second processing step called Preparation Date appears as an attribute to SUBSAMPLE.) The date can be approximate. If null, SAMPLE has not been processed or SAMPLE is not of a type that needs processing.

*Domain:* True or false. Can be Null. Default is false.

**1.9 Lithology:** A description of the lithology of the SAMPLE by the person who collected it.

*Domain:* Up to 80 characters. Default is blank.

**1.10 Lost Sample?:** True if SAMPLE is lost.

*Domain:* True or false. Not null. Default is false.

**1.11 Sample Comment:** Includes information on preservation, lost SAMPLEs, whether a SAMPLE was barren for calcareous nannoplankton, bryozoans, etc.

*Domain:* Up to 80 characters. Default is blank.

### 2 SUBSAMPLE (Supertype)

A group of fossils, such as foraminifera, calcareous nannoplankton, gastropods, or corals from a SAMPLE, or a collection for a paleomagnetic analysis. These are sent to members of the project with the corresponding specialization. Material remaining after one or more Subsamples are extracted is also considered a Subsample.

*Primary key:* Project Sample Number + Subsample Number
*Foreign key:* Project Sample Number

**2.1 Project Sample Number:** Tells from which SAMPLE the Subsample came.

*Domain:* Same as SAMPLE.Project Sample Number. Not null.

**2.2 Subsample Number:** A unique number starting from 1 for each Project Sample Number assigned by the data manager when the Subsample is prepared. In reports, the Subsample Number is connected to the Project Sample Number with a dash, *e.g.,* PSN000234-2.

*Domain:* Integers from 1 to 99. Not null.

**2.3 Taxon Type:** The code for a general group of taxa that are included in the Subsample. Different instances of SAMPLE.Type of Sample have different sets of Types of Subsample that are allowable.

For SAMPLE.Type of Sample = micro

| | |
|---|---|
| ben | benthic foraminifera faunal slide |
| pla | plankic foraminifera slide |
| nan | slide prepared for nannofossils |
| ost | ostracode slide |

For SAMPLE.Type of Sample = strib, basb, spec or float

| | |
|---|---|
| acor | ahermatypic corals |
| barn | barnacles |
| bry | bryozoans |
| cor | corals |
| clam | clams |
| crab | crabs |
| ech | echinoderms |
| hcor | hermatypic corals |
| mol | mollusks |
| sna | snails |

For SAMPLE.Type of Sample = micro, strib or basb

| | |
|---|---|
| orig | original sample material |
| wood | pieces of wood |

For SAMPLE.Type of Sample = pmag

| | |
|---|---|
| pmag | paleomagnetic sample |

*Domain:* The above codes, all lower case. Not null.

**2.4 Repository ID:** The code for the name of the institution where the Subsample is currently kept.

*Domain:* Five letters, all lower case. Not null.

**2.5 Curator ID:** The initials of the person responsible for the Subsample. If a participant's initials are not unique, the data manager will assign a code.

*Domain:* Four letters, all lower case. Not null.

**2.6 Transfer Date:** The date that the SUBSAMPLE was sent to the curator.

*Domain:* Same as SAMPLE.Sample Collection Date. Not null.

**2.7 Preparation Date:** The date a particular group was picked from washed residue of a micro, basb, or strib SAMPLE; was picked for a particular group; or the date a specimen or float SAMPLE was washed, glued, sorted, and/or put in boxes. If null, SAMPLE was not prepared.

*Domain:* Same as SAMPLE.Sample Collection Date. Default is null.

**2.8 Barren Subsample?:** True if a PROCESSED SAMPLE is found to have no fossils relevant to its Type of Subsample.

*Domain:* True or False. Default is False.

### 3 AGE DETERMINATION (Subtype of Subsample)

Planktic foraminifera and calcareous nannoplankton from a SAMPLE can be used to determine an age for a SITE. A paleomagnetic measurement of polarity, in conjunction with the local pattern of polarities from other SAMPLEs in the same stratigraphic sequence, can further refine the age. The geologic age returned may often not correspond exactly to that obtained from another Subsample, because of the limits of each dating system, but by combining them, the youngest and oldest possible ages may be determined even more precisely than the results of the individual determinations taken alone. There is substantial collaboration among the participants on individual SAMPLEs before they return their results.

*Primary key:* Project Sample Number + Subsample Number
*Foreign key:* Project Sample Number + Subsample Number

**3.1 Project Sample Number:** Tells to which SAMPLE the AGE DETERMINATION applies.

*Domain:* Same as SAMPLE.Project Sample Number. Not null.

**3.2 Subsample Number:** Together with Project Sample Number, tells which Subsample was used for the determination.

*Domain:* Same as Subsample.Subsample Number. Not null.

**3.3 Age Zone Determined:** The age determined by examination of a Subsample by a specialist. Usually, this is from calcareous nannoplankton, planktic foraminifera, or from a paleomagnetic sample combined with previous biochronologic results. The format of the returned age is variable. It can consist of a calcareous nannoplankton zone (*e.g.,* NN17), a planktic foraminifera zone (N12), an absolute age (3.5 Ma) or a range, consisting of any combination of these (NN16–NN17, 3.5 Ma–3.2 Ma, N12–3.5 Ma). Note that even a zone designation can include an absolute age if the proper index fossil is found (or not found) indicating that only a part of a zone is present in a SAMPLE. This format for ages is well established and easily understood by the users, but does not lend itself to SQL queries. Application specific functions (Youngest and Oldest) use the appropriate lookup table to find the currently established ages for zones and return either the youngest or the oldest age for any of the formats above. These functions are then used to fill in the derived attributes in the table corresponding to the AGE OF SITE entity.

*Domain:* 11 characters and digits, the minus sign, blank, and decimal. The letters are NN or N which must precede a two digit integer (with a leading zero if necessary), or Ma, which must precede a decimal number from 0.0 to 9.9. The minus sign is used as a connector when a range is given. Not null.

**3.4 Age Documentation Code:** The reference to the document submitted by a participant which contains his findings from a Subsample. All such documents are given a catalog number and stored as a paper record at several institutions.

*Domain:* Catalog number or numbers used for documents from participants.

**3.5 Age Entry Date:** The date that a value for Age Zone Determined was entered into the database, or if corrected or updated, the date of the last change. This information is used in conjunction with Date of Age Interpretation in the AGE entity to determine whether Youngest Age and Oldest Age need to be re-interpreted.

*Domain:* Same as SAMPLE.Sample Collection Date. Default is current date. Not null.

**3.6 Age Unreliable?:** Whether an AGE DETERMINATION is considered in error and not to be used in interpreting the age of a SITE. This attribute is marked as True in those cases.

*Domain:* True or False. Not null. Default is False.

**3.7 Age Comment:** Comments about the age determination.

*Domain:* 80 characters or numbers

### 4 ENVIRONMENT DETERMINATION (Subtype of Subsample)

Many types of Subsamples are used to determine the depositional environment for the SAMPLE. For some Subsamples, such as benthic foraminifera, a determination of paleowater depth is possible as well.

*Primary key:* Project Sample Number + Subsample Number

*Foreign key:* Project Sample Number + Subsample Number

**4.1 Project Sample Number:** Tells to which SAMPLE the ENVIRONMENT DETERMINATION applies.

**4.2 Subsample Number:** Together with Project Sample Number, tells which Subsample was used for the determination.

**4.3 Environment Determined:** The text of the ENVIRONMENT Determination returned by a participant. May be blank but only if Depth Determined is blank.

*Domain:* Up to 40 characters. Default is blank.

**4.4 Depth Determined:** The paleowater depth determination returned by a participant. Is blank if nothing is returned.

*Domain:* Up to 40 characters. Default is blank.

**4.5 Environment Documentation Code:** The reference to the document containing the findings from the SAMPLEs. (See note about these documents for AGE DETERMINATION.Age Documentation Code).

*Domain:* Catalog number, or numbers, for documents from participants.

**4.6 Environment Entry Date:** The date that a value for Environment Determined or Depth Determined was entered into the database, or if corrected or updated, the date of the last change to either. Both need to be considered together in interpreting the ENVIRONMENT of SITE.

*Domain:* Same as SAMPLE.Sample Collection Date. Default is current date. Not null.

**4.7 Environment Unreliable?:** Whether an ENVIRONMENT DETERMINATION is considered in error and not to be used in interpreting the ENVIRONMENT OF SITE. This attribute is marked as True if either Environment Determined or Depth Determined is not considered valid.

*Domain:* True or False. Not null. Default is False.

**4.8 Environment Comment:** Comments about Environment Determination or Depth Determination.

*Domain:* 80 characters or numbers

## 5 TAXON OCCURRENCE

An observation that a particular taxon was found in a Subsample. There is a one-to-many relationship between Subsample and TAXON OCCURRENCE. All of the TAXON OCCURRENCEs taken together for a given Subsample can be considered a species list for that subsample.

*Primary key:* Project Sample Number + Subsample Number + Taxon Type + Original Taxon ID
*Foreign key:* Project Sample Number + Subsample Number
*Foreign key:* Taxon Type + Original Taxon ID

**5.1 Project Sample Number:** Tells the Project Sample Number in which this TAXON OCCURRENCE was found.

*Domain:* Same as SAMPLE.Project Sample Number

**5.2 Subsample Number:** Together with Project Sample Number, tells the Subsample in which this TAXON OCCURRENCE was found.

*Domain:* Same as Subsample.Subsample Number

**5.3 Original Taxon ID:** Together with Taxon Type, identifies a taxon that was observed to occur in the Subsample, using the taxon name in use at the time of the observation. It is not uncommon for the name of a particular taxon to change as more taxonomic information about it is changed, and to avoid confusion, the original name is recorded here. The Original Taxon ID, and that taxon's full name, is resolved by the many to one relationship to TAXON NAME, and by that entity's many to one relationship to itself.

*Domain:* Same as TAXON NAME.Original Taxon ID

**5.4 Taxon Type:** Tells the code for the group of taxa being searched for in the Subsample. Researchers working on different groups of taxa may inadvertently use the same Original or Current Taxon ID for different taxa. To avoid confusion, Taxon Type is made part of the key so that identifiers for taxa need only be unique within a particular group.

*Domain:* Same as Subsample.Taxon Type

**5.5 Abundance Code:** A collector specific estimate of abundance in the SAMPLE, appropriate for the particular taxon and Type of Subsample.

*Domain:* 12 characters and/or numbers.

## 6 TAXON NAME

Taxa identified in a SAMPLE are given a code which is used to record their occurrence. This entity records this code, the Original Taxon ID, and the full name which it represents. The code may represent the name of a family, a genus, species and subspecies or even an informal designation, such as "urchin spine" or "unknown coral fragment".

Using a full genus and species appellation for recording and entering species observed in a SAMPLE, and for analyzing the data afterwards, is both time consuming and error prone. Here, eight-letter abbreviations are used in the database. Experience shows that this is long enough so that a person familiar with a particular group can easily decipher it, yet not so short that it is ambiguous. Often, scientific names differ in only one or two letters out of many. It is easier to check whether one of 8 letters is in error than to see if one of 20 letters is in error. In producing summary reports for internal use and when reviewing the names on a computer screen, eight-letter abbreviations are much easier to read and to format into tables. A good data entry program should require typing only one to three letters to enter the full eight-letter code automatically.

To keep track of changes to the currently used name for a taxon, this entity enters into a recursive relationship with itself, using Taxon Type + Current Taxon ID as a foreign key to look up the current full name of any taxon recorded in the database.

This method of resolving the currently used name of a taxon is not a substitute for a taxonomic database (*e.g.*, Paleobank, Krebs *et al.*, 1996). Maintenance of this data cannot be done automatically by accessing such taxonomic databases, since most changes to Current Taxon ID will be to record the substitution of a scientific name for an informal designation of a taxon, or the correction of an error in identification. It is the responsibility of each researcher to maintain the names of the taxon with which he is working.

*Primary key:* Taxon Type + Original Taxon ID
*Foreign key:* Taxon Type + Current Taxon ID. This foreign key is used in a one to many recursive relationship to resolve the Current Taxon ID given the Original Taxon ID. Because Original and Current Taxon ID are unique only within a given Taxon Type, Taxon Type is a necessary part of the key for resolving these relationships.

6.1 **Original Taxon ID:** An abbreviation representing the taxonomic name used at the time a particular specimen is recorded. This name will never be changed so that the name in the database will always refer to what is actually written down on the original data sheet. This avoids confusion in case the name currently used changes several times.

*Domain:* Eight letters, both upper and lower case, and digits 0 to 9. Spaces and punctuation are not allowed and the first character cannot be a digit. These restrictions allow the abbreviation to be used as legal field (column) names for the most commonly used databases.

6.2 **Current Taxon ID:** Tells the currently used abbreviation for a given taxon. Often, a researcher will change the name for a taxon, either to correct an error in identification, to reflect a more precise identification, or because of a change in the taxonomy. By recording the currently used name for an obsolete name, the new name can automatically be used when reports are printed. Merely substituting the new code for the old in the database can cause great confusion and destroys information about the history of names used for a particular taxon.

The rules for changing the Current Taxon ID are as follows:

> Whenever Current Taxon ID is changed for an existing Original Taxon ID, a new instance must be added to this entity. This new instance must have the same value for both Original Taxon ID and Current Taxon ID. The other information in the original instance, including Name1, Name2, and Name3, is left unchanged to preserve the history of changes to the Original Taxon ID and its full name. If yet another change is made to Current Taxon ID, then another instance is added and both previous instances must have Current Taxon ID updated. There is a recursive relationship between this entity and itself which allows a reference to the Original Taxon ID to return the Current Taxon ID, along with the current full name. All instances then, where Original Taxon ID and Current Taxon ID are different represent obsolete usages. To prevent ambiguity in archived species lists, the combination of Taxon Type and Taxon ID, even for obsolete usages, must remain unique. This means that an Original Taxon ID, such as Coralsp, cannot be recycled for use with a different taxon, once a more accurate identification is supplied for the original usage.

*Domain:* Same as Original Taxon ID.

**6.3 Taxon Type:** The taxon or group of taxa for which a set of unique Taxon IDs is constructed and maintained by a researcher

*Domain:* Same as Subsample.Taxon Type

**6.4 Name1:** A genus name, a higher taxonomic name, or a short unstructured description.

*Domain:* Not Null. Up to 20 letters. Can include '?'.

**6.5 Name2:** A species name, the letters 'sp.' possibly with a letter or number after, or a continuation of a short description from Name 1.

*Domain:* Up to 20 letters. Can include '?'. Default is blank.

**6.6 Name3:** A subspecies name, the letters 'ssp.' possibly with a letter or number after, or a continuation of a short description from Name1. Name1, Name2, and Name3 taken together are referred to in this paper as the full name.

*Domain:* Up to 20 letters. Can include '?'. Default is blank.

## 7 SITE VISIT (Supertype)

A visit to a single SITE by one or more persons at the same time where one or more SAMPLEs are taken. If two people taking different kinds of SAMPLEs agree that their SAMPLEs are equivalent in age because of their close proximity on the outcrop they are considered to be from the same SITE VISIT. Since SAMPLEs are considered equivalent in age if their upper and lower ranges in the section are the same, if one SAMPLE spans only a small part of the vertical extent of another SAMPLE, such as a microfossil sample taken next to a very large coral head, then the two SAMPLEs are considered to be from different SITE VISITs. It is also possible that two SAMPLEs are taken that are of equivalent age but that fact may not be known to the data manager when the Site Visit Number is assigned, and they will receive different Site Visit Numbers.

The primary key for SITE VISIT, Site Visit Number, is also known as the PPP_Number and is used to identify collections in published work.

*Primary key:* Site Visit Number (PPP_number)

**7.1 Site Visit Number:** The code assigned to the SITE VISIT. Having one number for all SAMPLEs corresponding to the same time range in the section facilitates reference to the age ultimately returned by the collectors of those SAMPLEs by providing a publishable number at an early stage. It is possible that two SAMPLEs collected at exactly the same time and place could receive different Site Visit Numbers because of the way they were handled during collection and subsequent processing.

*Domain:* PPP-000001 to PPP-999999

**7.2 Site Number:** Tells to which SITE the SITE VISIT belongs.

*Domain:* The set of existing SITE VISIT numbers, but with the prefix S instead of PPP.

## 8 FORMER SITE VISIT NUMBER (Subtype of SITE VISIT)

Early in the project, SAMPLEs were assigned what was called a "default CJ number" to identify the same entity that the SITE VISIT number now identifies. Older labels on stored SAMPLEs and references in field notes use this code. An even earlier code, not used on sample labels, may be found in Coates' field notes.

*Primary key:* Site Visit Number

**8.1 Site Visit Number:** Tells to which SITE VISIT the FORMER SITE VISIT NUMBER refers.

*Domain:* 12 characters. Not null.

**8.2 Former Site Visit Number:** The "Default CJ number" on some labels and in some field notes. No longer assigned.

*Domain:* 12 characters Default is blank.

**8.3 Obsolete Site Visit Number:** The code found only in Coates' early field notes. No longer assigned.

*Domain:* 12 characters. Default is blank.

## 9 SITE OVERLAP

A correspondence between a current SITE VISIT and an earlier or concurrent instance of a SITE VISIT to that SITE or to an adjacent SITE. Examples of a correspondence are: a current SITE VISIT being considered exactly the same as another; a current SITE VISIT being a subset or superset of another; or a current SITE VISIT being close to but not overlapping another.

This entity is used to produce user views of the data with equivalent and closely associated SITE VISITs listed close to each other to aid in grouping the SAMPLEs by time interval.

**9.1 Overlap Documentation Code:** An identifier for a written note describing how the current Site Visit is related to another. Normally, the note is from a field notebook and the owner, volume, page, and line numbers are given. This field must be unique, but is otherwise unstructured.

*Domain:* 20 letters or numbers. Not null.

**9.2 Current Site Visit Number:** Tells which current SITE VISIT has entered into an association.

*Domain:* Same as SITE VISIT.Site Visit Numbers.

**9.3 Referenced Site Visit Number:** Tells which SITE VISIT is referred to in documentation about a previous, or a concurrent, SITE VISIT.

*Domain:* Same as SITE VISIT.Site Visit Codes.

**9.4 Overlap Type:** How the two SITE VISITs are associated. The judgement of how the collections are related is made by the person collecting the SAMPLE. Sometimes a collection of macrofossils will be made from a SITE visited the previous year and these will be considered "equivalent" and an Overlap Type will be assigned indicating this. The codes are:

| | |
|---|---|
| equiv | The current SITE VISIT is considered equivalent to another one. |
| part | The current SITE VISIT is a part, or a subset, of another one. |
| cont | The current SITE VISIT contains, or is a superset, of another one. |
| near | The current SITE VISIT is close to but not overlapping another one. |

*Domain:* The above codes, all lower case. Not null.

## 10 SITE (Supertype)

A part of an outcrop from which one or more SAMPLEs have been taken, all having the same upper and lower stratigraphic boundaries. The lateral extent of the SITE can be as large as feasible while still maintaining the same upper and lower boundaries. Typically, microfossil sample SITEs are six centimeters or less in extent while some bulk, float, and specimen sample SITEs may extend for tens of meters along a bedding plane and be a meter or so in stratigraphic thickness.

If a return visit is made to a site after an extended period of time and additional SAMPLEs (bulk, specimen, *etc.*) are collected, the collector may record that the site was the same as that visited previously. But micro samples are normally too small and too precise in their upper and lower bounds to be considered equivalent if collected at different times, so the collector will generally record that the new SITE is near but not exactly the same as a previous collection.

The code for identifying the SITE uses the digital part of the Site Visit Code from the first visit, preceded by the letter 'S'. If the SAMPLE is being collected for the first time this will have the same digital component as the Site Visit Code. (*e.g.,* PPP001234 and S001234).

*Primary key:* Site Number
*Foreign key:* Section Number
*Foreign key:* Stratigraphic Unit ID
*Foreign key:* Locality Number
*Foreign key:* Correlated Site Code

**10.1 Site Number:** Tells which SITE was visited. The default indicates that no Site Number has been assigned. Site Numbers are assigned in batches, after the data for new SAMPLES have been entered.

*Domain:* Same as SITE VISIT.Site Visit Number except that the digital part is preceded by 'S' instead of 'PPP'. Default is 'S000000'.

**10.2 Section Number:** Tells the STRATIGRAPHIC SECTION in which the SITE was found.

*Domain:* Same as STRATIGRAPHIC SECTION.Section Number. Default is 0.

**10.3 Stratigraphic Unit ID:** Tells from which STRATIGRAPHIC UNIT a SAMPLE was taken.

*Domain:* Same as STRATIGRAPHIC UNIT.-Stratigraphic Unit ID. Not null.

**10.4 Locality Number:** Tells the LOCALITY in which a SITE is found.

*Domain:* Same as LOCALITY.Locality Number. Not null.

**10.5 Correlated Site Code:** Tells to which CORRELATED SITE this SITE has been assigned.

*Domain:* Same as CORRELATED SITE.Correlated Site Number

**10.6 Position in Section:** The position of the SITE in the composite section, measured in meters from the bottom and adjusted for dip and local differences in section thickness.

*Domain:* Numbers from 0.0 to 999.9. Not null.

**10.7 Latitude:** The latitude of the SITE, using decimal notation, as accurately as can be measured. Currently, location is measured to within 100 m using a map or a GPS receiver. Latitude and longitude can be expressed in degrees, minutes, and seconds where required by using a function to make the conversion on the fly.

*Domain:* Numbers from −4.00000 to 15.00000 and 999. Default is 999, indicating a missing value.

**10.8 Longitude:** The longitude of the SITE, using decimal notation, as accurately as can be measured.

*Domain:* Numbers from −88.00000 to −60.00000, and 999. Default is 999, indicating a missing value.

## 11 STRATIGRAPHIC SECTION

A diagram showing the stratigraphic relationship among SITEs, to scale. The Chief Stratigrapher will decide which SITEs can be grouped together into any given STRATIGRAPHIC SECTION. A SITE may belong to only one STRATIGRAPHIC SECTION, or it may remain ungrouped.

*Primary key:* Section Number

**11.1 Section Number:** The number assigned to the STRATIGRAPHIC SECTION.

*Domain:* Integers from 0 to 999. Default is 0.

**11.2 Section Name:** A name given to the STRATIGRAPHIC SECTION

*Domain:* Up to 20 characters. Not null.

**11.3 Depositional Basin:** A geographic area with a common river drainage.

*Domain:* Up to 20 characters. Not null.

## 12 STRATIGRAPHIC UNIT

The smallest established subdivision of the rocks in the study area.

*Primary key:* Stratigraphic Unit ID

**12.1 Stratigraphic Unit ID:** A code identifying the Stratigraphic Group, Stratigraphic Formation, and Stratigraphic Member. Since formation names are unique in the study area, the code consists of an abbreviation of the formation name, and if used, the member name. Includes a code for unknown.

*Domain:* Up to 12 characters.

**12.2 Stratigraphic Group:** The established name of the group. Can be ‘unknown’. Blank indicates that a group name is not used. (The simple name “Group” cannot be used because ‘group’ is a reserved word used by SQL, the query language used by all relational databases.)

*Domain:* Stratigraphic Group names. Default is blank.

**12.3 Stratigraphic Formation:** The established name of the formation. Can be ‘unknown’. Cannot be blank.

*Domain:* Stratigraphic Formation names. Not null.

**12.4 Stratigraphic Member:** The established name of the member. Can be ‘unknown’. Blank indicates that a member name is not used.

*Domain:* Stratigraphic Member names. Default is blank.

**12.5 Stratigraphic Sequence:** A decimal number indicating the position of the STRATIGRAPHIC UNIT in the geological column. It is used to display the names in stratigraphic rather than alphabetic order. The smallest numbers correspond to the youngest rocks. Blank is 0, ‘unknown’ is 99.9.

*Domain:* Integers from 1.0 to 99.9. Not null.

## 13 LOCALITY

The local area where the outcrop is found. The location of an outcrop is described by a reference to a place name (Locality Name) that can be found on a topographic map. To further define the location, a Detailed Locality is used which consists of short directions on how to reach a particular outcrop. Together, they generally locate the outcrop to within about 100 meters. More than one SITE can be found in a given LOCALITY.

*Primary key:* Locality Number

**13.1 Locality Number:** A unique number assigned to each LOCALITY.

*Domain:* Five digits, 0–9. Not 00000 and not null.

**13.2 Locality Name:** A name that can be found on a 1:50000 topographic map (such as Isla Colon or Rio Azul) which identifies a small area.

*Domain:* Any name on a map up to 20 characters.

**13.3 Detailed Locality:** Short directions on how to reach the outcrop. Examples are “300 meters north of the bridge over the Rio Azul” or “50 m downstream from Site PPP000123”

*Domain:* Up to 80 characters.

**13.4 Country ID:** An abbreviation that tells the country in which the SITE is found. The abbreviations currently in use are:

Pan (Panama), CR (Costa Rica), Nic (Nicaragua), Ecu (Ecuador), Tri (Trinidad & Tobago), Ven (Venezuela).

*Domain:* The above codes. Not null.

13.5 **Region ID:** A subdivision of a country.

*Domain:* Established names of subdivisions of countries, or an abbreviation for them. Up to 12 characters.

13.6 **Ocean ID:** An abbreviation that tells into which ocean the streams flow.

*Domain:* P (Pacific) or C (Caribbean). Not null.

## 14 AGE OF SITE (Subtype of SITE)

The composite geologic age of a specific SITE, as interpreted from the information returned from AGE DETERMINATIONs. Sometimes this information is contradictory so that the AGE OF SITE cannot be calculated automatically from individual AGE DETERMINATIONs. It requires an experienced researcher to make the final interpretation. Available valid ages from nannoplankton, forams, and paleomagnetic analyses are presented to the person making this interpretation, as well as the maximum and minimum possible ages in millions of years. These are listed as derived attributes in this entity since the information is available elsewhere in the database. In cases where there is no direct information about a SITE, an AGE is interpolated from the position of the SITE relative to nearby directly dated SITEs.

*Primary key:* Site Number

*Foreign key:* Site Number

14.1 **Site Number:** Tells to which SITE the AGE OF SITE refers.

*Domain:* Same as SITE.Site Number. Not null.

14.2 **Youngest Age:** The youngest composite age in Ma interpreted for a SITE by an experienced researcher.

*Domain:* Decimals from 0.0 to 9.9.

14.3 **Oldest Age:** The oldest composite age in Ma interpreted for a SITE by an experienced researcher.

*Domain:* Decimals from 0.0 to 9.9

14.4 **Age Interpreter:** The initials of the person who made the age interpretation.

*Domain:* Same as SAMPLE.Collector ID. Not Null

14.5 **Date of Age Interpretation:** The date the interpretation was made. If this date is earlier than the date that any AGE DETERMINATION was last entered into the database for this SITE, the AGEs will have to be reinterpreted.

*Domain:* Same as SAMPLE.Sample Collection Date. Not null.

14.6 **Interpolated?:** Whether the AGE OF SITEs were obtained by interpolation from other nearby SITEs.

*Domain:* True or false. Default is false.

14.7 **Age Comment:** Comments about the dating process.

*Domain:* Up to 80 characters. Default is blank.

## 15 ENVIRONMENT OF SITE (Subtype of SITE)

The composite depositional environment for a specific SITE including paleowater depth. Like AGE OF SITE, an experienced researcher is needed to make the final interpretation from all available reports of AGE DETERMINATION.

*Primary key:* Site Number

*Foreign key:* Site Number

15.1 **Site Number:** Tells which SITE has this environment.

*Domain:* Same as SITE.Site Number. Not null.

15.2 **Paleodepth:** The determination of the depth of the water at the time of deposition for the SITE. This is an uncoded attribute, reflecting concisely the best estimate of the Environment Interpreter.

*Domain:* Up to 20 characters. Default is blank.

15.3 **Paleoenvironment:** The depositional environment, excluding depth, for the SITE. This is an uncoded attribute, reflecting concisely the best estimate of the Environment Interpreter.

*Domain:* Up to 80 characters. Default is blank.

15.4 **Environment Interpreter:** The experienced participant making the interpretation of both Paleodepth and Paleoenvironment.

*Domain:* Same as SAMPLE.Collector ID. Not null.

15.5 **Date of Environment Interpretation:** The date the interpretation of the ENVIRONMENT was made. This information will be used in conjunction with ENVIRONMENT DETERMINATION.Table Entry Date to determine if a re-interpretation is necessary.

*Domain:* Same as Sample.Sample Collection Date. Not null.

**15.6 Environment Comment:** Comments about the interpretation of the ENVIRONMENT.

*Domain:* Up to 80 characters. Default is blank.

### 16 CORRELATED SITE

A group of SITEs with similar AGEs. The Chief Stratigrapher will group SITEs to provide coarser divisions of time for the use of project participants.

*Primary key:* Correlated Site Number

**16.1 Correlated Site Code:** A code identifying a group of similarly aged SITEs.

*Domain:* Integers from 1 to 999.

**16.2 Defined Youngest Age:** The youngest age, in Ma, of SITEs assigned to the CORRELATED SITE.

*Domain:* Decimals from 0.0 to 9.9. Not null.

**16.3 Defined Oldest Age:** The oldest age, in Ma, of SITEs assigned to the CORRELATED SITE.

*Domain:* Decimals from 0.0 to 9.9.

### Definitions

The following words are used consistently in the names of entities and attributes to modify the remainder of the name.

| | |
|---|---|
| code: | A set of letters and numbers associated with an attribute or entity. |
| ID: | A code which is a short abbreviation of a longer name and which is designed to be easily identifiable by a user familiar with the domain of entities or attributes that it describes. |
| number: | A code consisting primarily of digits, sometimes with a fixed set of letters added to the beginning, assigned in numerical order. |
| type: | One of a short set of codes used to describe a particular class of attributes. |
| date: | A particular calendar day. Dates refer to events connected with the activities of the PPP participants, not to geological events. |
| age: | Time expressed in millions of years before the present. |
| age zone: | Time expressed either as a microfossil zone, a geological age, or in millions of years before the present. |
| ?: | This symbol at the end of the name of an attribute indicates that the attribute takes on logical values, true or false. |

## ACKNOWLEDGMENTS

The original design of the PPP Database was by Karl Kaufmann and Laurel Collins. Subsequent modifications included substantial input by Laurel Collins. Helena Fortunata assisted generously in developing the early stages of the model. The database is available at the internet Web site http://www.fiu.edu/˜collinsl/.

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1989. Handbook of Relational Database Design. Addison Wesley. Reading, Massachusetts. 839 pp.

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1996. Paleobank, A Relational Database for Invertebrate Paleontology: The Data Model. The University of Kansas Paleontological Contributions, New Series, #8. The University of Kansas, Lawrence, Kansas. 7 pp.

**Teorey, T.J.**
1990. Database Modeling and Design: The entity-relationship approach. Morgan Kaufmann, San Mateo, California, 267 pp.

# APPENDIX A

## MAPS

ANTHONY G. COATES
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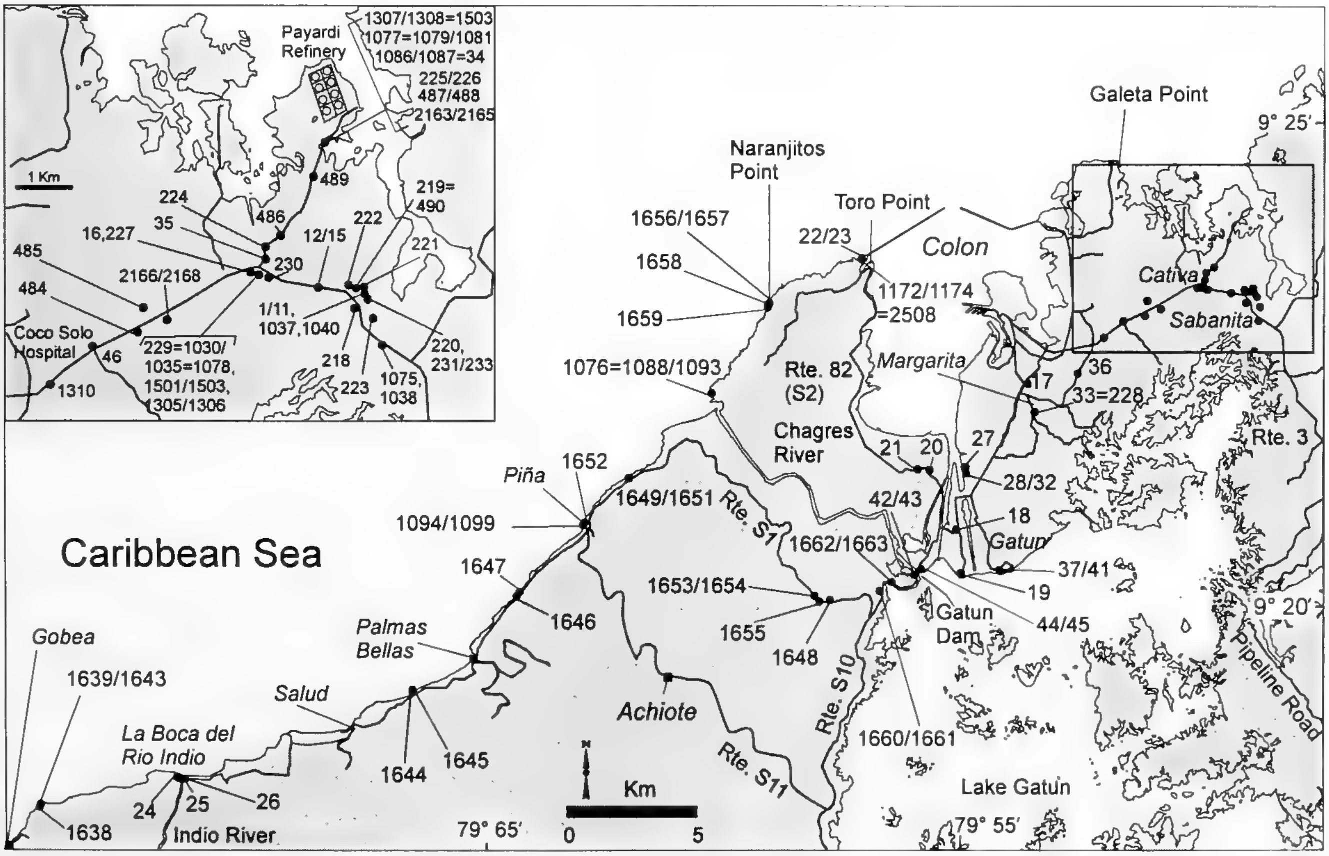
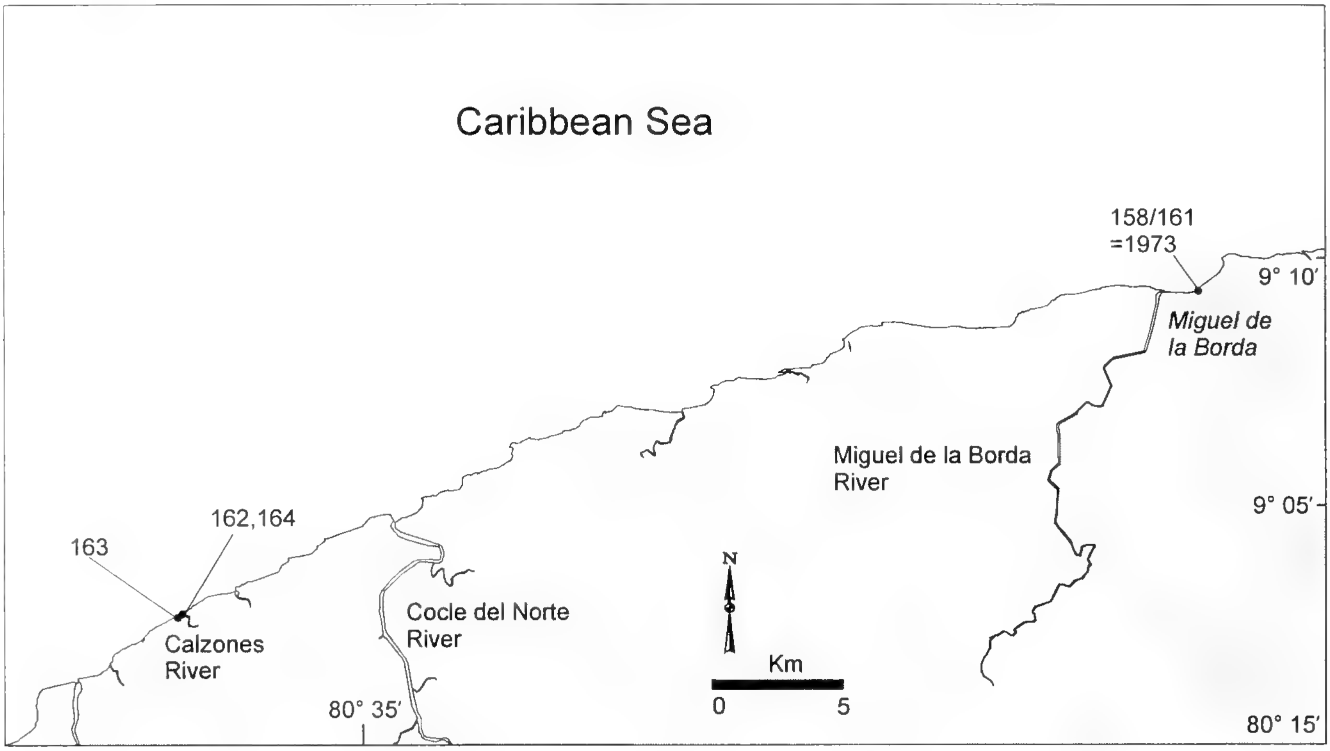
These maps were produced with the computer programs Atlas Geographic Information System, version 2.1, and Coreldraw, version 7.0. They include PPP numbers for all Caribbean sampling localities to date. The maps are listed below by number in the order presented.

Map 1. Colon to Gobea, Panama
Map 2. Miguel de la Borda to Calzones River, Panama
Map 3. Petaquilla River to Boca de Concepcion, Panama
Map 4 & Insets. Escudo de Veraguas, Panama, and insets A, B, C and D
Map 5. Valiente Peninsula, Panama
Insets of Map 5. Insets A, B, C, D, E and F
Map 6. Cayo Agua, Panama
Map 7. Popa Island, Panama
Insets of Map 6. Insets A, B, C, D, E, F, G and H
Map 8. Bastimentos Island, Panama
Map 9. Colon Island, Panama
Map 10. Manzanillo Point to Bonifacio, Costa Rica.
Map 11. Bananito River to Limon, Costa Rica
Inset A of Map 11. Portete to Chocolate Creek
Inset B of Map 11. Cangrejos to Route 32
Inset C of Map 11. Banano River to Vizcaya River

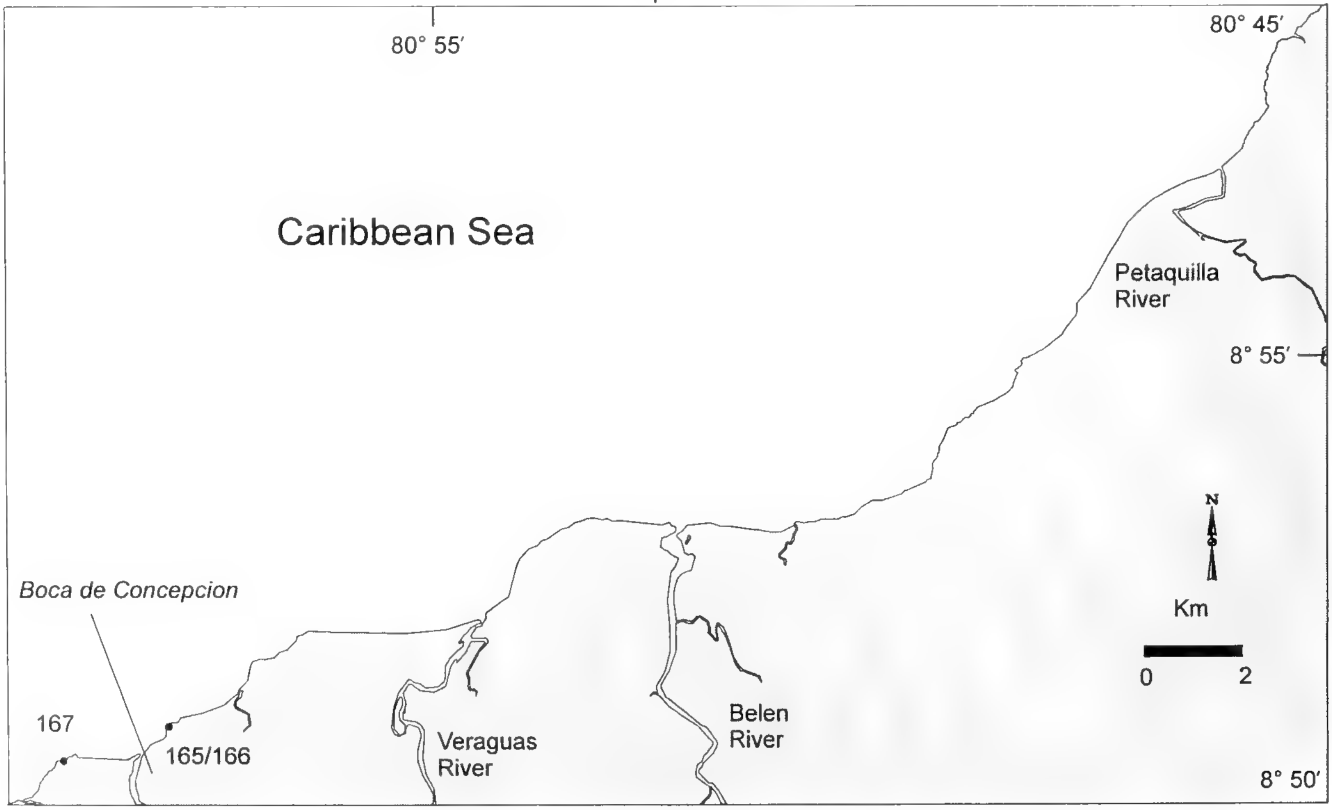
Map 1



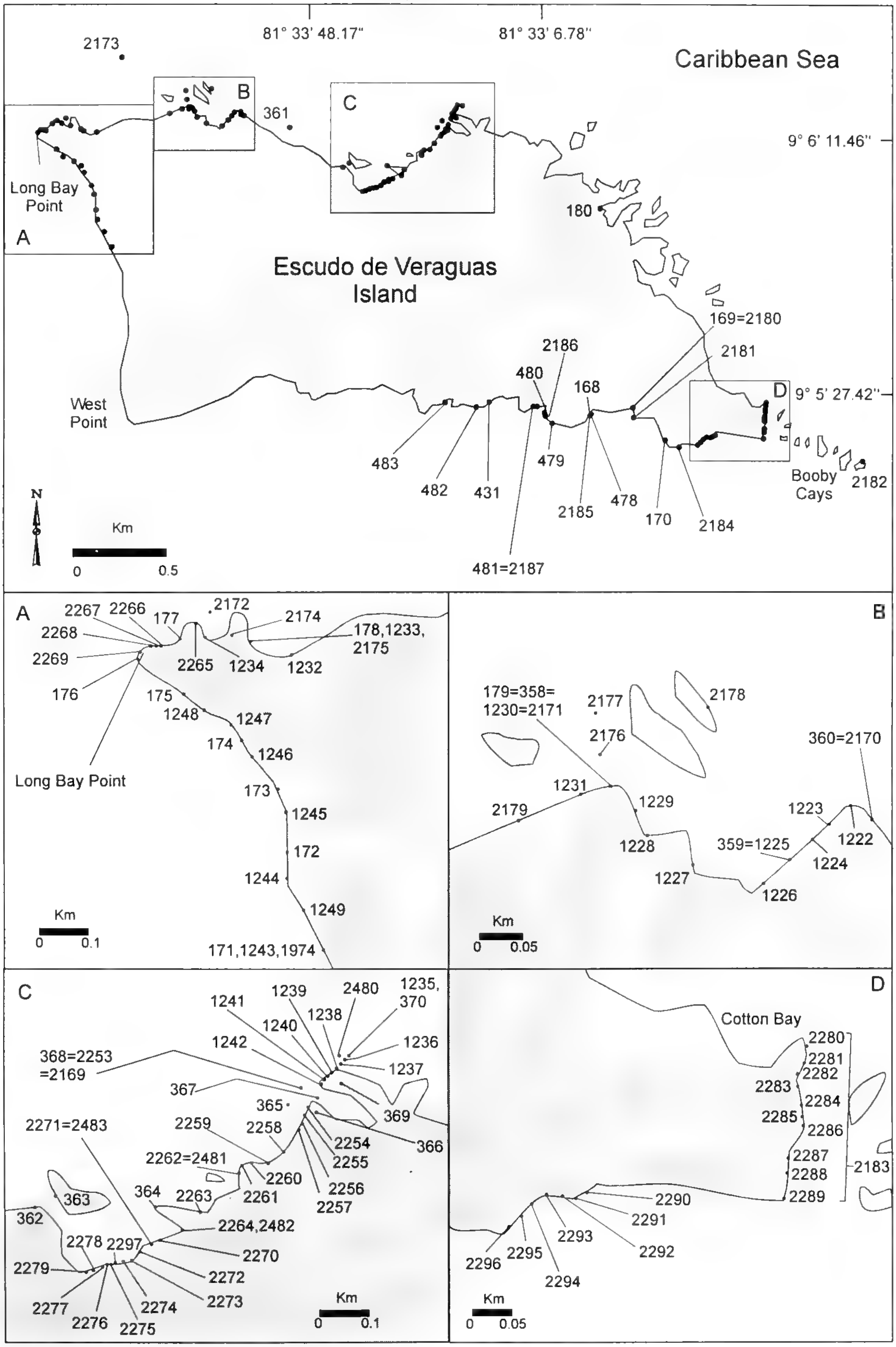
Map 2


Caribbean Sea
158/161
=1973
9° 10′
Miguel de
la Borda
Miguel de la Borda
River
9° 05′
162,164
163
Calzones
River
Cocle del Norte
River
N
Km
0
5
80° 35′
80° 15′

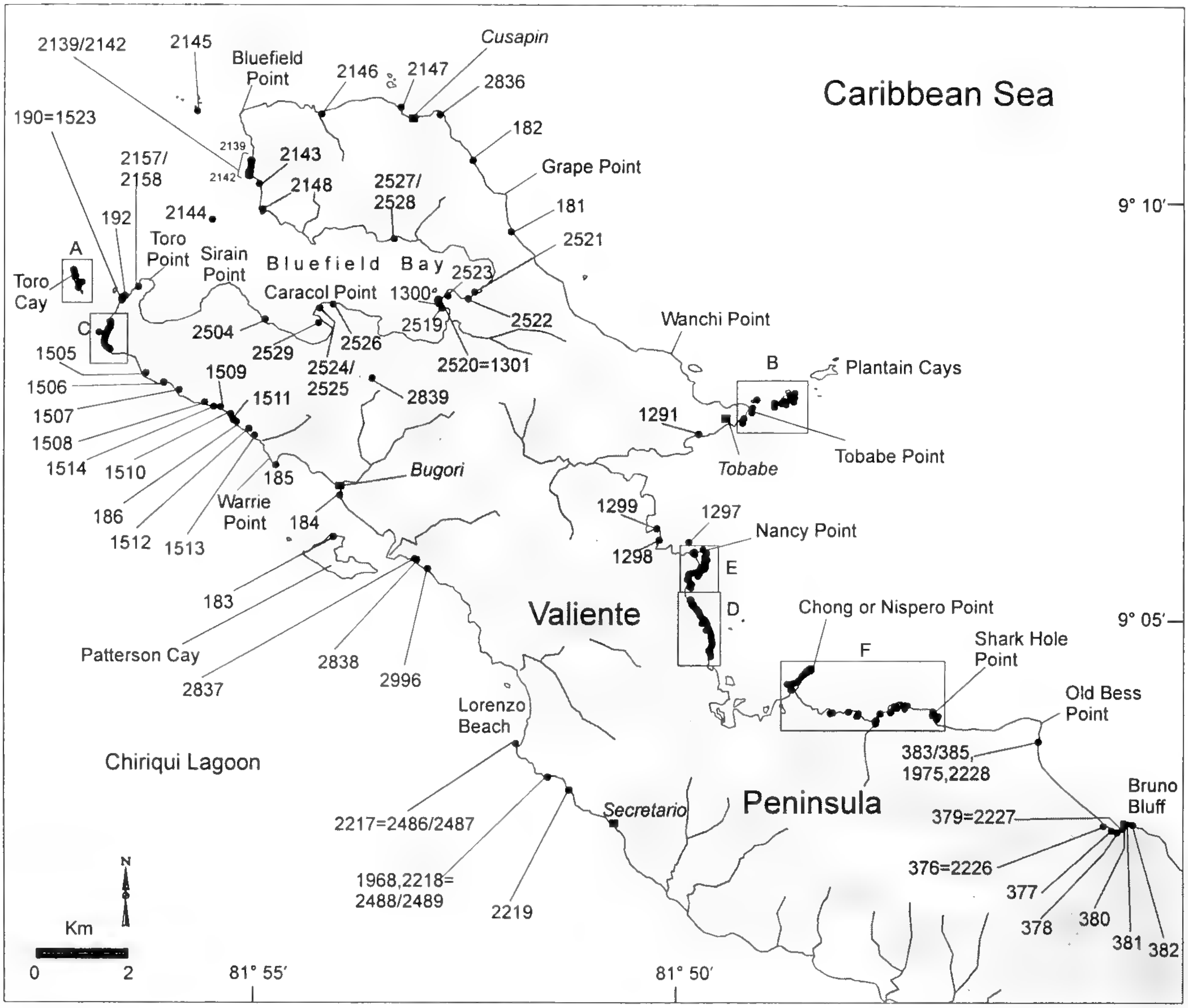
Map 3


80° 55′
80° 45′
Caribbean Sea
Petaquilla
River
8° 55′
N
Km
0
2
Boca de Concepcion
167
165/166
Veraguas
River
Belen
River
8° 50′

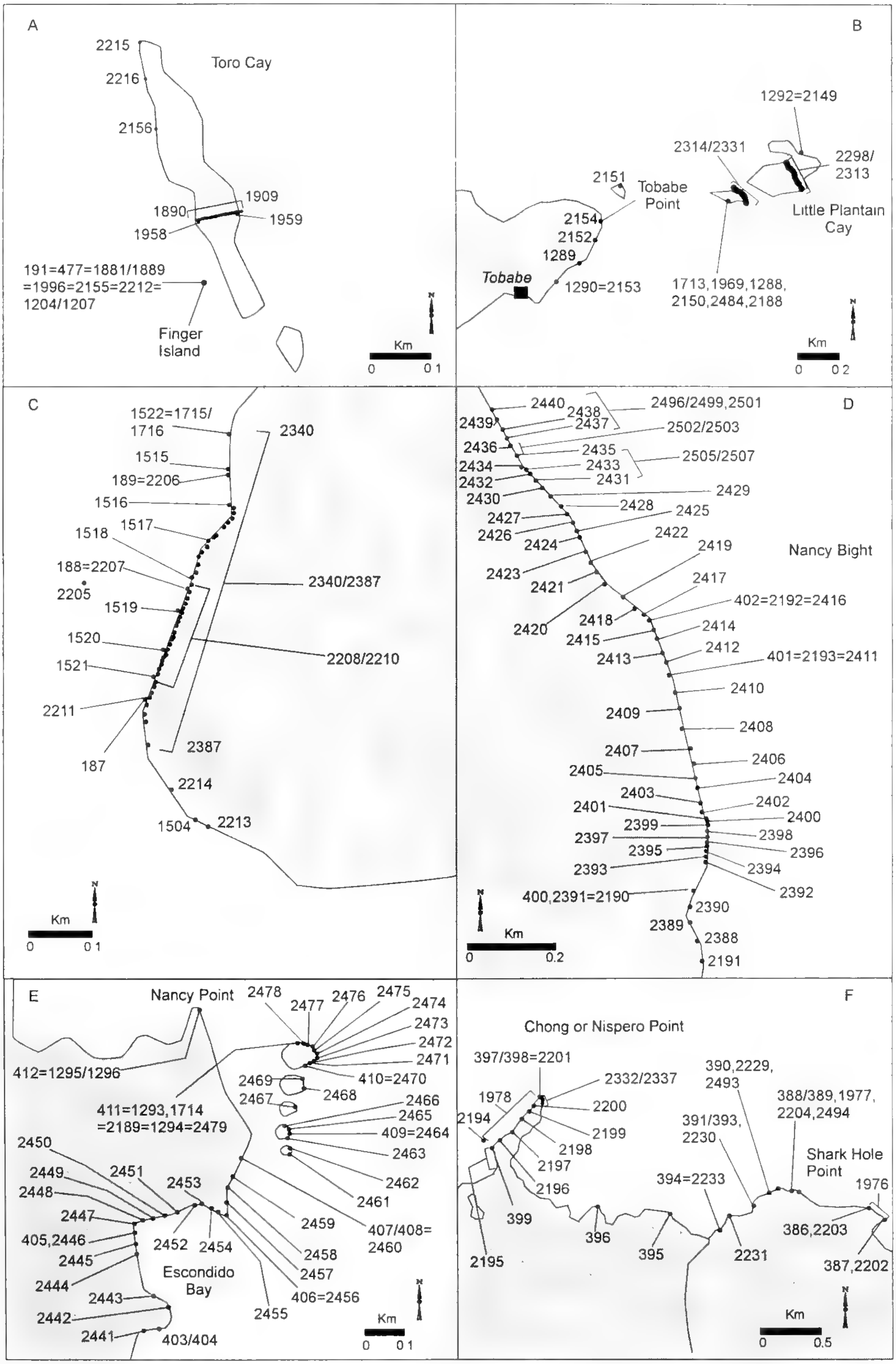
Map 4 & Insets


81° 33' 48.17"
81° 33' 6.78"
9° 6' 11.46"
9° 5' 27.42"
Caribbean Sea
Escudo de Veraguas Island
2173
361
180
Long Bay Point
West Point
A
B
C
D
169=2180
2181
2186
480
168
483
482
431
479
2185
478
170
2184
481=2187
Booby Cays
2182
N
Km
0
0.5
A
2267
2266
177
2172
2174
2268
178,1233,
2175
2269
2265
1234
1232
176
175
1248
1247
174
1246
Long Bay Point
173
1245
172
1244
1249
171,1243,1974
Km
0
0.1
B
179=358=
1230=2171
2177
2178
2176
360=2170
1231
1229
2179
1223
1228
359=1225
1222
1224
1227
1226
Km
0
0.05
C
1239
2480
1235,
370
1241
1238
1240
1236
1242
368=2253
=2169
1237
367
365
369
2271=2483
2259
2258
2254
366
2255
2262=2481
2260
2256
363
364
2263
2261
2257
362
2264,2482
2278
2297
2270
2279
2272
2273
2277
2274
2276
2275
Km
0
0.1
D
Cotton Bay
2280
2281
2282
2283
2284
2285
2286
2287
2183
2288
2289
2290
2291
2293
2292
2296
2295
2294
Km
0
0.05

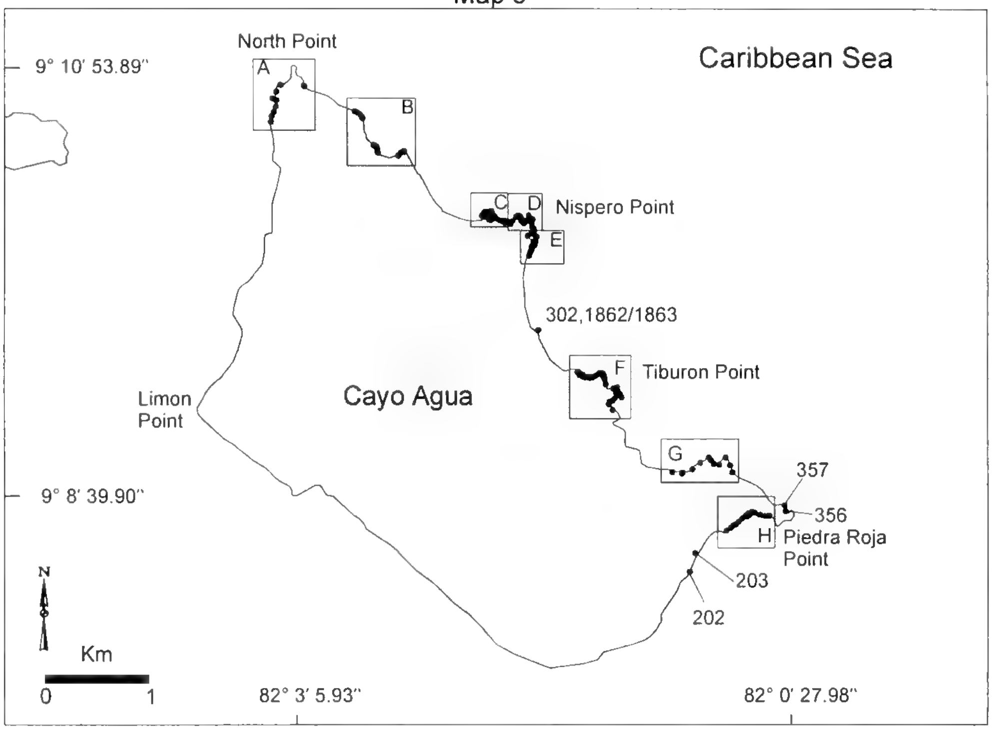
Map 5


2139/2142
2145
Bluefield Point
2146
2147
Cusapin
2836
Caribbean Sea
190=1523
2139
2142
2143
182
2157/2158
2148
2527/2528
Grape Point
192
2144
181
9° 10′
A
Toro Point
Sirain Point
Bluefield Bay
2521
Toro Cay
2523
C
Caracol Point
1300
2504
2526
2519
2522
1505
2529
Wanchi Point
1509
2524/2525
2520=1301
B
Plantain Cays
1506
1511
2839
1507
1291
1508
Tobabe
Tobabe Point
1514
1510
Bugori
185
Warrie Point
186
184
1299
1297
1512
1513
Nancy Point
1298
E
183
Valiente
D
Chong or Nispero Point
9° 05′
Patterson Cay
2838
F
Shark Hole Point
2837
2996
Old Bess Point
Lorenzo Beach
Chiriqui Lagoon
383/385, 1975,2228
Bruno Bluff
2217=2486/2487
Secretario
Peninsula
379=2227
376=2226
1968,2218=2488/2489
377
N
2219
378
380
Km
381
382
0
2
81° 55′
81° 50′

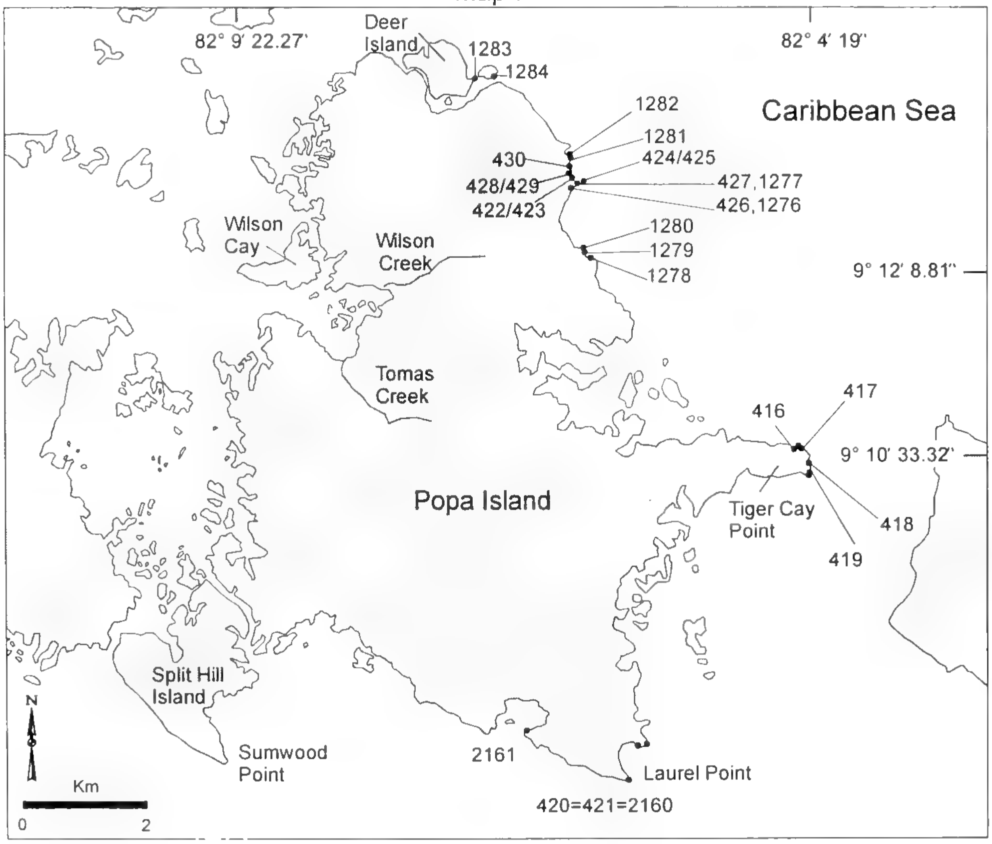
Insets of Map 5



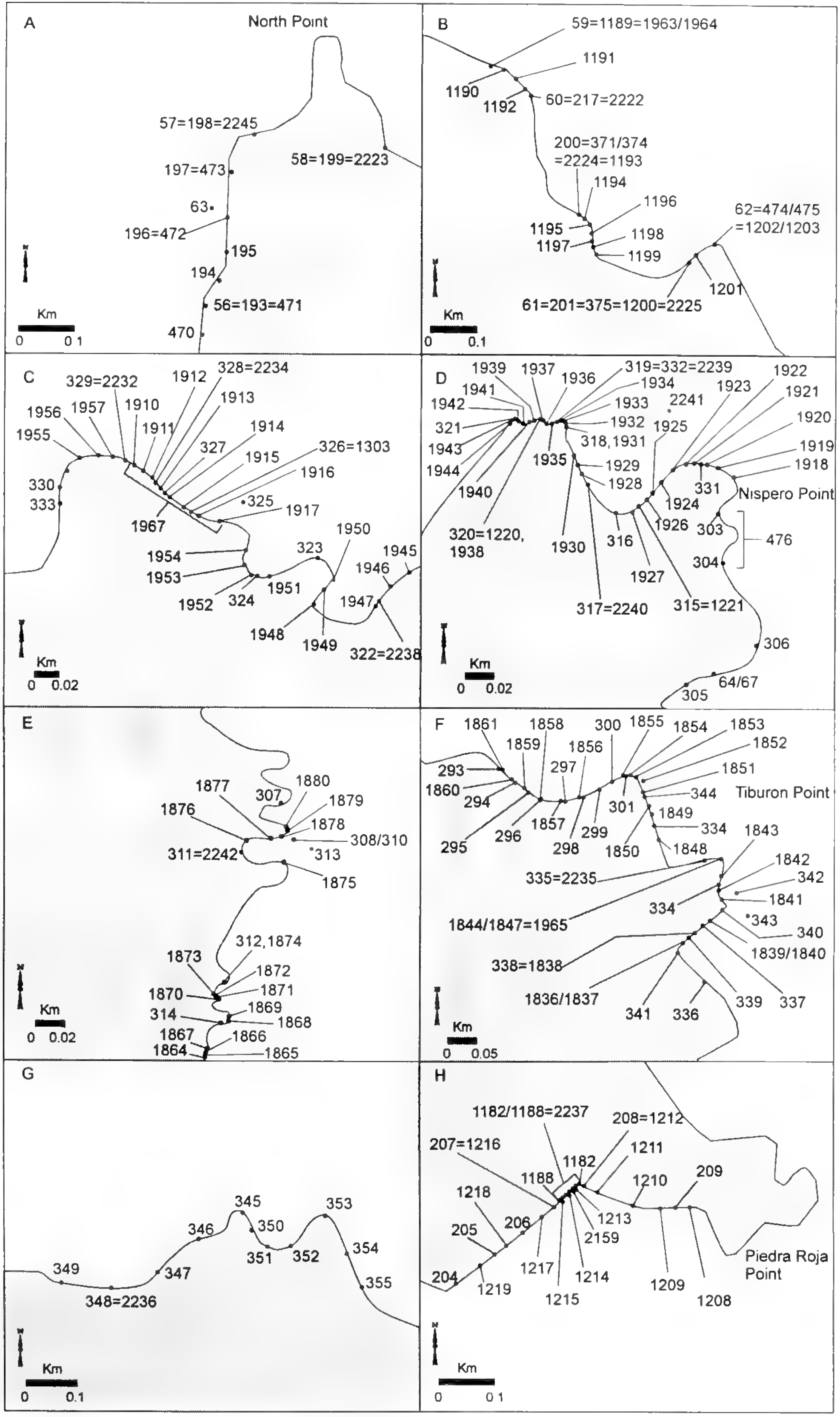
Map 6


North Point
9° 10′ 53.89″
Caribbean Sea
A
B
C
D
Nispero Point
E
302,1862/1863
F
Tiburon Point
Cayo Agua
Limon Point
G
357
9° 8′ 39.90″
356
H
Piedra Roja Point
203
202
N
Km
0
1
82° 3′ 5.93″
82° 0′ 27.98″

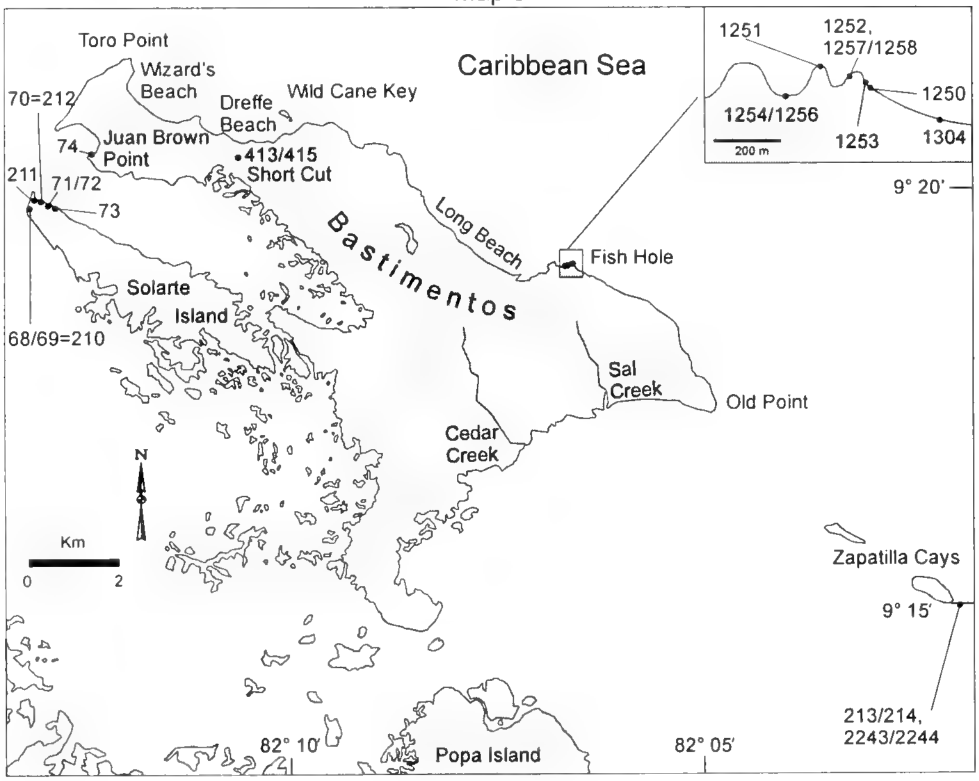
Map 7


82° 9′ 22.27″
Deer Island
1283
1284
82° 4′ 19″
1282
Caribbean Sea
1281
430
424/425
428/429
427,1277
422/423
426,1276
Wilson Cay
Wilson Creek
1280
1279
1278
9° 12′ 8.81″
Tomas Creek
417
416
9° 10′ 33.32″
Popa Island
Tiger Cay Point
418
419
Split Hill Island
N
Sumwood Point
2161
Laurel Point
Km
0
2
420=421=2160

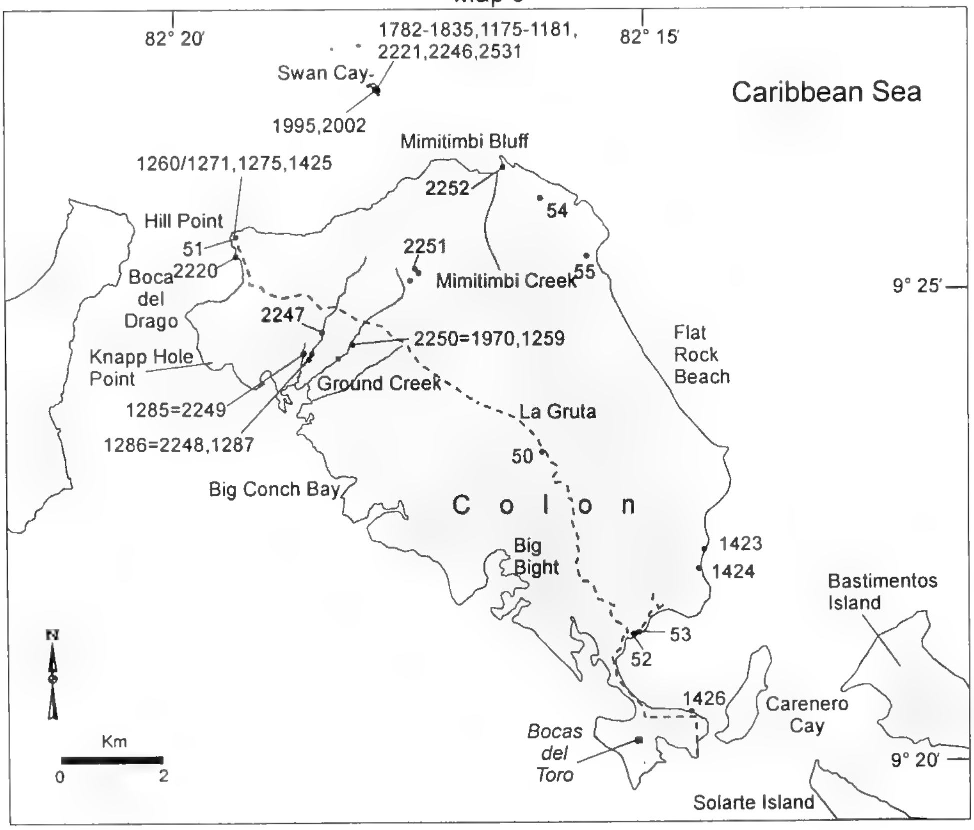
Insets of Map 6



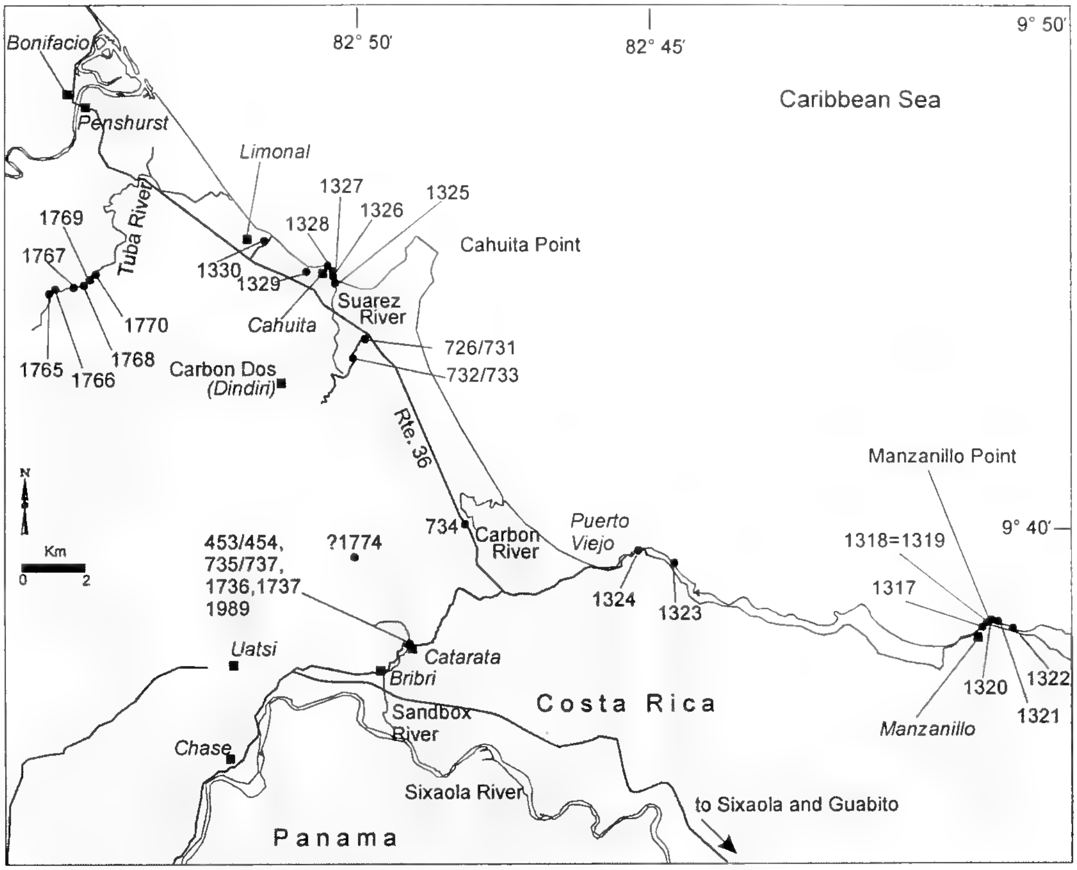
Map 8


Caribbean Sea
Toro Point
Wizard's Beach
70=212
Dreffe Beach
Wild Cane Key
74
Juan Brown Point
•413/415
Short Cut
211
71/72
73
Bastimentos
Long Beach
Fish Hole
Solarte Island
68/69=210
Sal Creek
Old Point
Cedar Creek
N
Km
0
2
Zapatilla Cays
9° 20′
9° 15′
213/214,
2243/2244
82° 10′
82° 05′
Popa Island
1251
1252,
1257/1258
1250
1254/1256
1253
1304
200 m

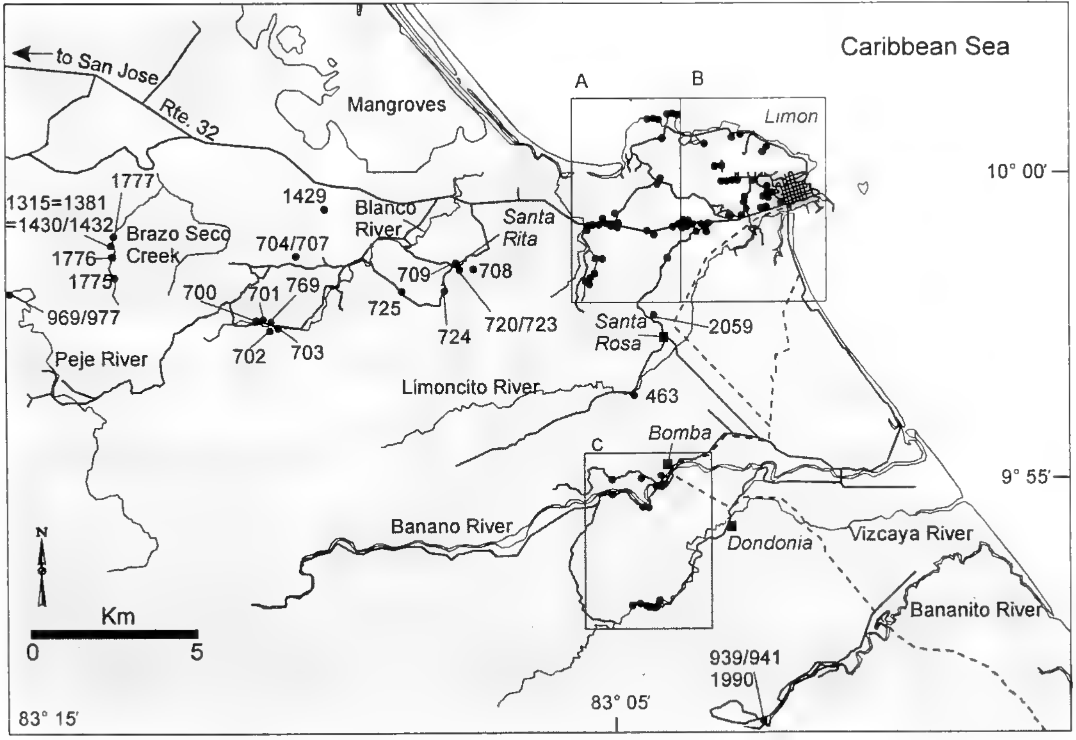
Map 9


82° 20′
82° 15′
1782-1835,1175-1181,
2221,2246,2531
Swan Cay
1995,2002
Caribbean Sea
Mimitimbi Bluff
1260/1271,1275,1425
2252
54
Hill Point
51
2220
Boca del Drago
2251
Mimitimbi Creek
55
9° 25′
2247
2250=1970,1259
Flat Rock Beach
Knapp Hole Point
Ground Creek
La Gruta
1285=2249
1286=2248,1287
50
Big Conch Bay
C o l o n
Big Bight
1423
1424
Bastimentos Island
53
52
1426
Carenero Cay
Bocas del Toro
9° 20′
Solarte Island
N
Km
0
2

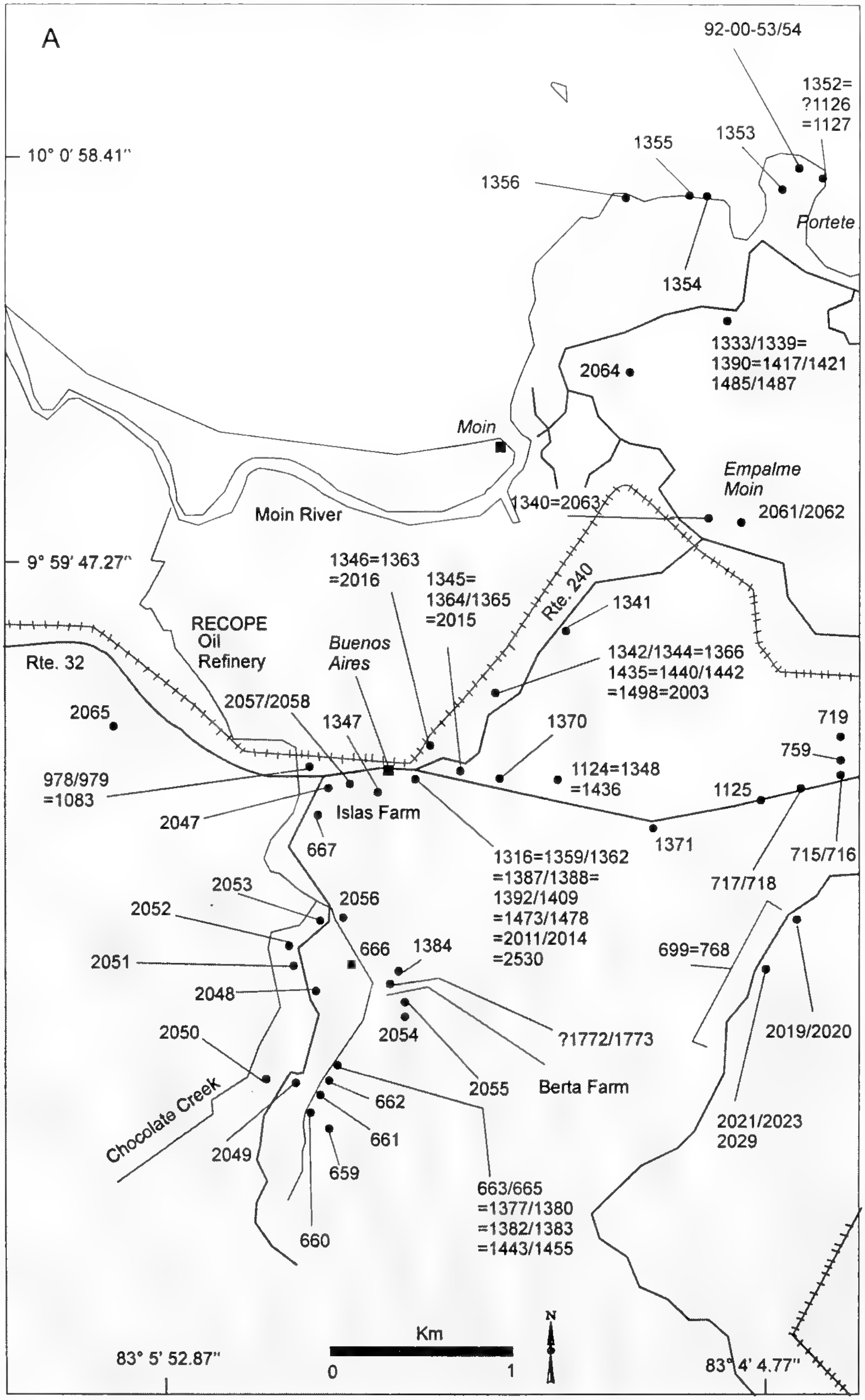
Map 10


82° 50′
82° 45′
9° 50′
Caribbean Sea
Bonifacio
Penshurst
Limonal
1327
1325
1326
1328
1769
Tuba River
Cahuita Point
1767
1330
1329
Suarez River
Cahuita
1770
726/731
732/733
1765
1766
1768
Carbon Dos (Dindiri)
Rte. 36
Manzanillo Point
N
Km
0 2
453/454, 735/737, 1736,1737 1989
?1774
734
Carbon River
Puerto Viejo
1318=1319
9° 40′
1317
1324
1323
Uatsi
Catarata
Bribri
Sandbox River
Costa Rica
1320
1322
1321
Manzanillo
Chase
Sixaola River
to Sixaola and Guabito
Panama

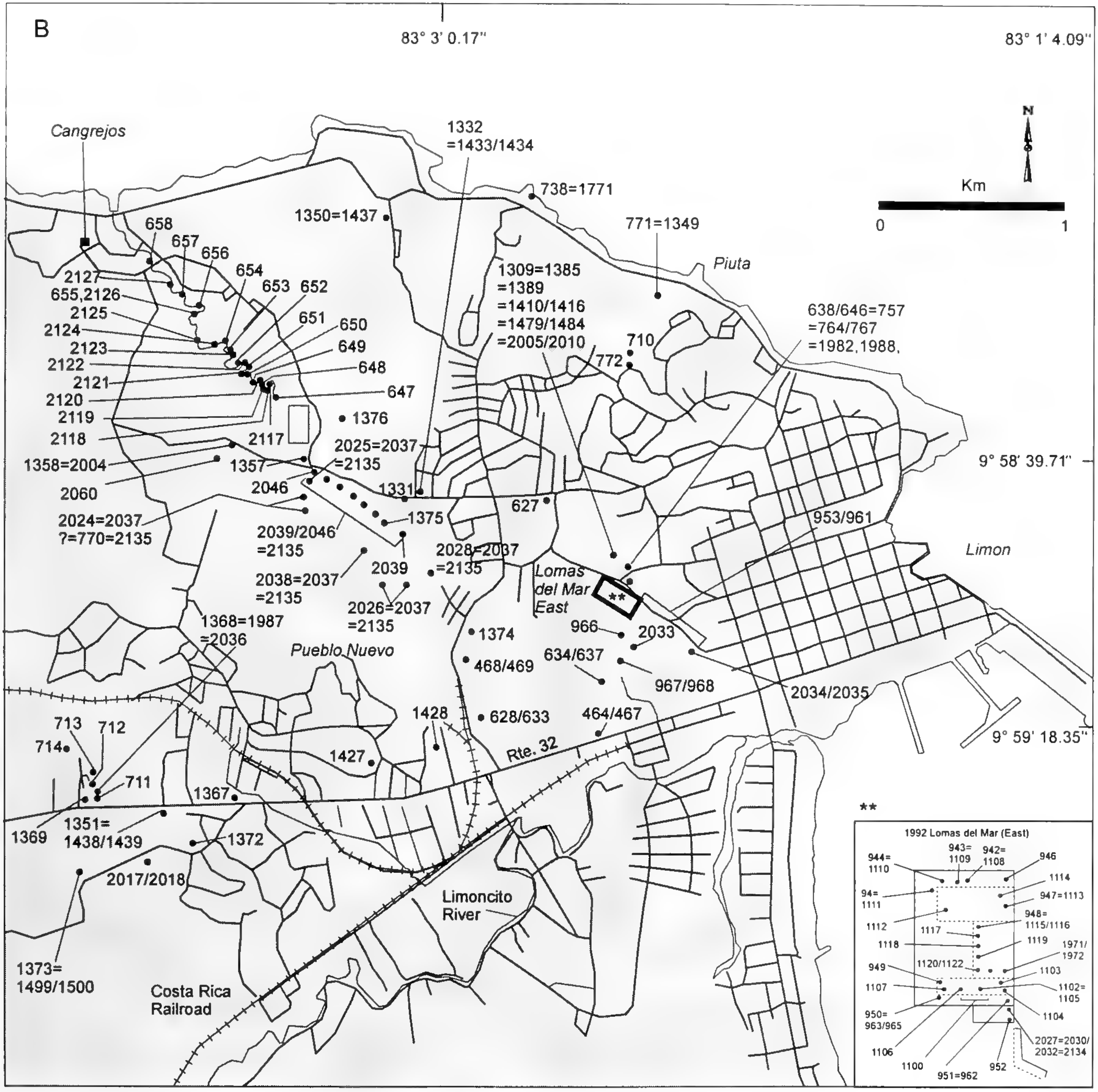
Map 11


to San Jose
Caribbean Sea
Rte. 32
A
B
Mangroves
Limon
10° 00′
1777
1315=1381 =1430/1432
1429
Blanco River
Santa Rita
Brazo Seco Creek
704/707
1776
1775
709
708
700
701
769
725
969/977
720/723
724
Santa Rosa
2059
702
703
Peje River
Limoncito River
463
Bomba
C
9° 55′
N
Banano River
Dondonia
Vizcaya River
Km
0 5
Bananito River
939/941 1990
83° 15′
83° 05′

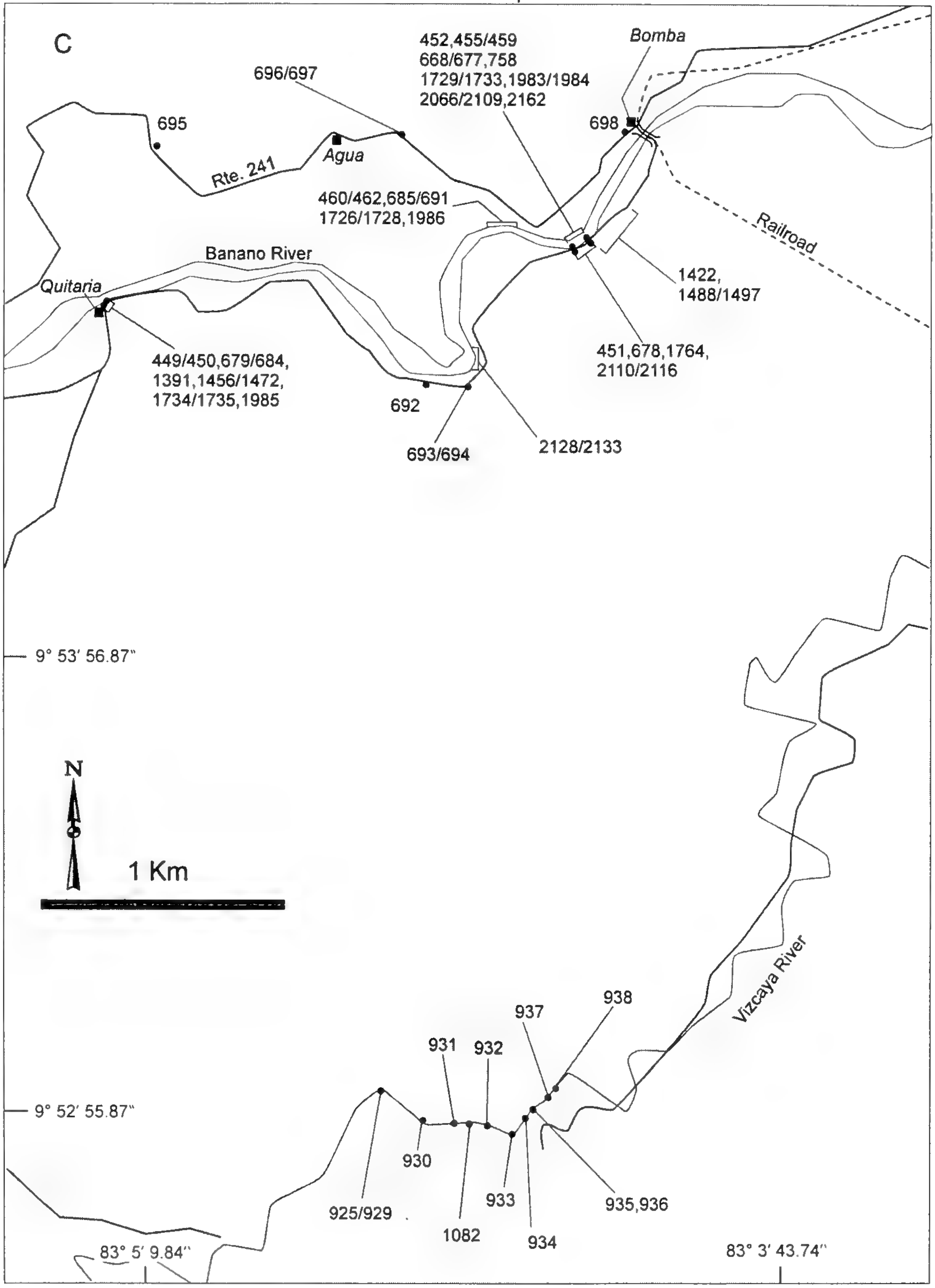
Inset A of Map 11



Inset B of Map 11



Inset C of Map 11



# APPENDIX B

## STRATIGRAPHIC SECTIONS

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Smithsonian Institution
Smithsonian Tropical Research Institute
Washington, D.C. 20560-0580, U.S.A.

The stratigraphic sections listed below were drawn with the computer program Logger version 5.0 (Rockworks, 1991), and include PPP numbers for all Caribbean sampling localities to date.

### PANAMA CANAL BASIN

1. Sabanita to Payardi
2. Margarita to Gatun
3. Toro Point
4. Piña
5. Rio Indio
6. Miguel de la Borda, 1 km to the East
7. Boca de Concepcion, 0.5 km to the East
8. Concepcion, 0.8 km to the West at Zapato Bluffs
9. Calzones River, Eastern and Western Sections

### BOCAS DEL TORO BASIN

10. Escudo de Veraguas, Northern Coast
11. Escudo de Veraguas, Southeastern Coast
12. Valiente Peninsula, Bruno Bluff to Plantain Cays
13. Valiente Peninsula, Toro Point
14. Valiente Peninsula, Toro Cays
15. Valiente Peninsula, Southern Coast
16. Cayo Agua, North Point, Western Side
17. Cayo Agua, Piedra Roja Point, Western Sequence
18. Cayo Agua, Piedra Roja Point, Eastern Sequence
19. Cayo Agua, North Point to Tiburon Point
20. Cayo Agua, South Nispero Point
21. Bastimentos Island, Short Cut
22. Bastimentos Island, Fish Hole, Eastern Sequence
23. Bastimentos Island, Fish Hole, Western Sequence
24. Solarte Cay, Western Tip
25. Swan Cay, North of Colon Island
26. Colon Island, Hill Point

### LIMON BASIN

27. Sandbox River
28. Carbon Dos (Dindiri)
29. Banano River
30. Peje River
31. Bananito River
32. Santa Rita
33. Chocolate to Buenos Aires
34. Empalme
35. Pueblo Nuevo, Cemetery
36. Lomas del Mar, Eastern Sequence
37. Lomas del Mar, Western Reef Flank Sequence
38. Lomas del Mar, Western Reef Tract Sequence
39. Vizcaya River

### KEY TO SYMBOLS

| | |
|---|---|
| 2471 | PPP numbers, which are assigned to PPP collecting sites*. They are referenced in the PPP Database, which can be accessed at the internet site http://www.fiu.edu/˜collinsl/ |
| ■ | Sample collected within measured section |
| ● | Sample not collected within measured section but correlated to its approximate stratigraphic level from nearby exposures |
| [ | All samples within bracket were collected from the same horizon |
| I | Sample was collected from various stratigraphic horizons within this range |
| ▲ | Paleomagnetic sample was collected within measured section |
| △ | Paleomagenetic sample not collected within measured section but correlated to its approximate stratigraphic level from nearby exposure |
| R | Paleomagnetic sample with reversed polarity |
| N | Paleomagnetic sample with normal polarity |
| ? | Paleomagnetic sample with indeterminate polarity |

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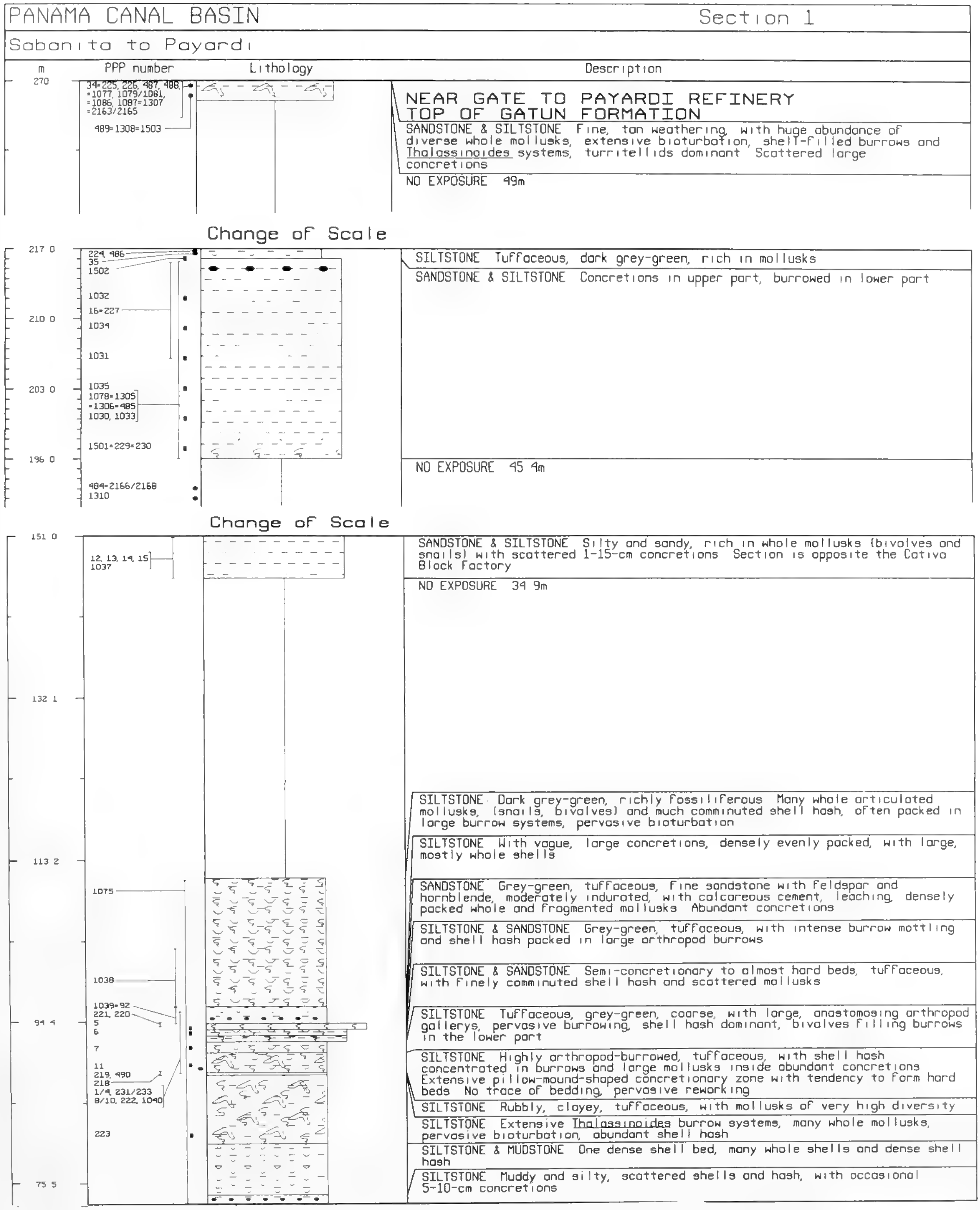
* When PPP numbers are given as a range, *e.g.*, 2471/2476, the first number is the highest and the second the lowest stratigraphically.

# Key to Lithologies and Sedimentary Structures



NEAR GATE TO PAYARDI REFINERY
TOP OF GATUN FORMATION

SANDSTONE & SILTSTONE Fine, tan weathering, with huge abundance of diverse whole mollusks, extensive bioturbation, shell-filled burrows and *Thalassinoides* systems, turritellids dominant Scattered large concretions

NO EXPOSURE 49m

SILTSTONE Tuffaceous, dark grey-green, rich in mollusks

SANDSTONE & SILTSTONE Concretions in upper part, burrowed in lower part

NO EXPOSURE 45 4m

SANDSTONE & SILTSTONE Silty and sandy, rich in whole mollusks (bivalves and snails) with scattered 1-15-cm concretions Section is opposite the Cativa Block Factory

NO EXPOSURE 34 9m

SILTSTONE Dark grey-green, richly fossiliferous Many whole articulated mollusks, (snails, bivalves) and much comminuted shell hash, often packed in large burrow systems, pervasive bioturbation

SILTSTONE With vague, large concretions, densely evenly packed, with large, mostly whole shells

SANDSTONE Grey-green, tuffaceous, fine sandstone with feldspar and hornblende, moderately indurated, with calcareous cement, leaching, densely packed whole and fragmented mollusks Abundant concretions

SILTSTONE & SANDSTONE Grey-green, tuffaceous, with intense burrow mottling and shell hash packed in large arthropod burrows

SILTSTONE & SANDSTONE Semi-concretionary to almost hard beds, tuffaceous, with finely comminuted shell hash and scattered mollusks

SILTSTONE Tuffaceous, grey-green, coarse, with large, anastomosing arthropod gallerys, pervasive burrowing, shell hash dominant, bivalves filling burrows in the lower part

SILTSTONE Highly arthropod-burrowed, tuffaceous, with shell hash concentrated in burrows and large mollusks inside abundant concretions Extensive pillow-mound-shaped concretionary zone with tendency to form hard beds No trace of bedding, pervasive reworking

SILTSTONE Rubbly, clayey, tuffaceous, with mollusks of very high diversity

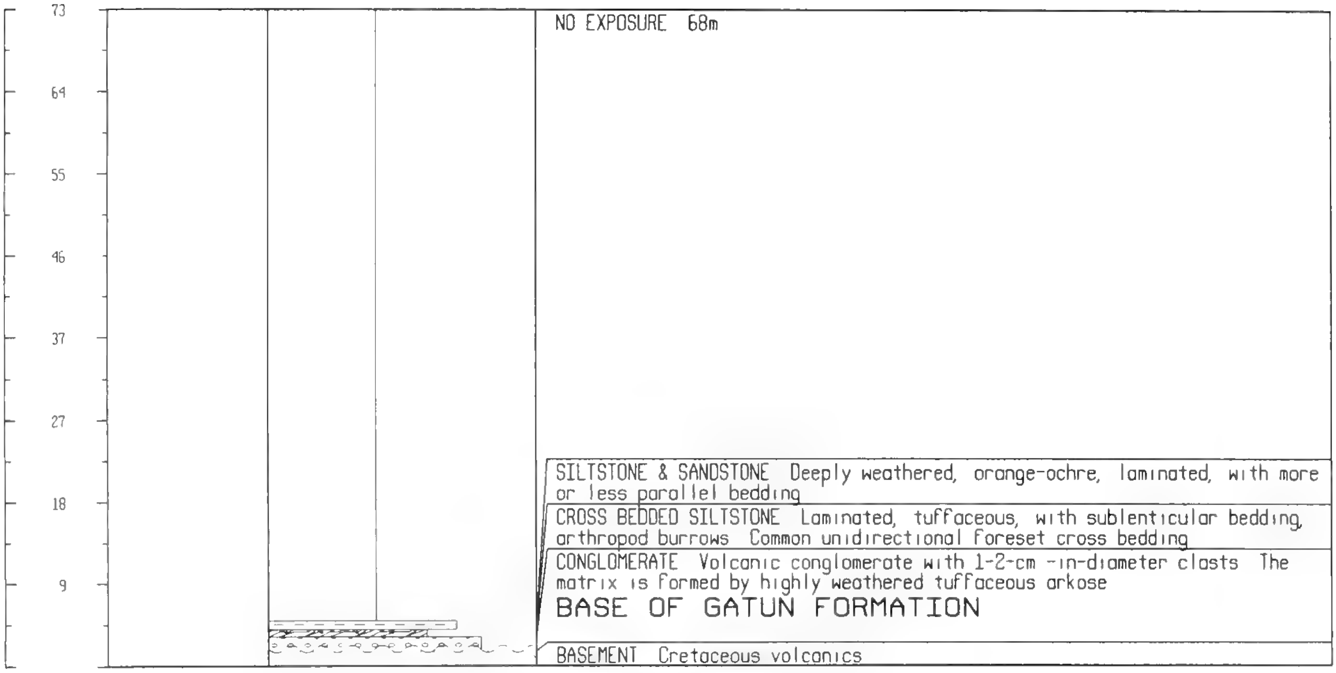
SILTSTONE Extensive *Thalassinoides* burrow systems, many whole mollusks, pervasive bioturbation, abundant shell hash

SILTSTONE & MUDSTONE One dense shell bed, many whole shells and dense shell hash

SILTSTONE Muddy and silty, scattered shells and hash, with occasional 5-10-cm concretions

Change of Scale

Section 1, contd.



NO EXPOSURE 68m

SILTSTONE & SANDSTONE Deeply weathered, orange-ochre, laminated, with more or less parallel bedding

CROSS BEDDED SILTSTONE Laminated, tuffaceous, with sublenticular bedding, arthropod burrows Common unidirectional foreset cross bedding

CONGLOMERATE Volcanic conglomerate with 1-2-cm -in-diameter clasts The matrix is formed by highly weathered tuffaceous arkose

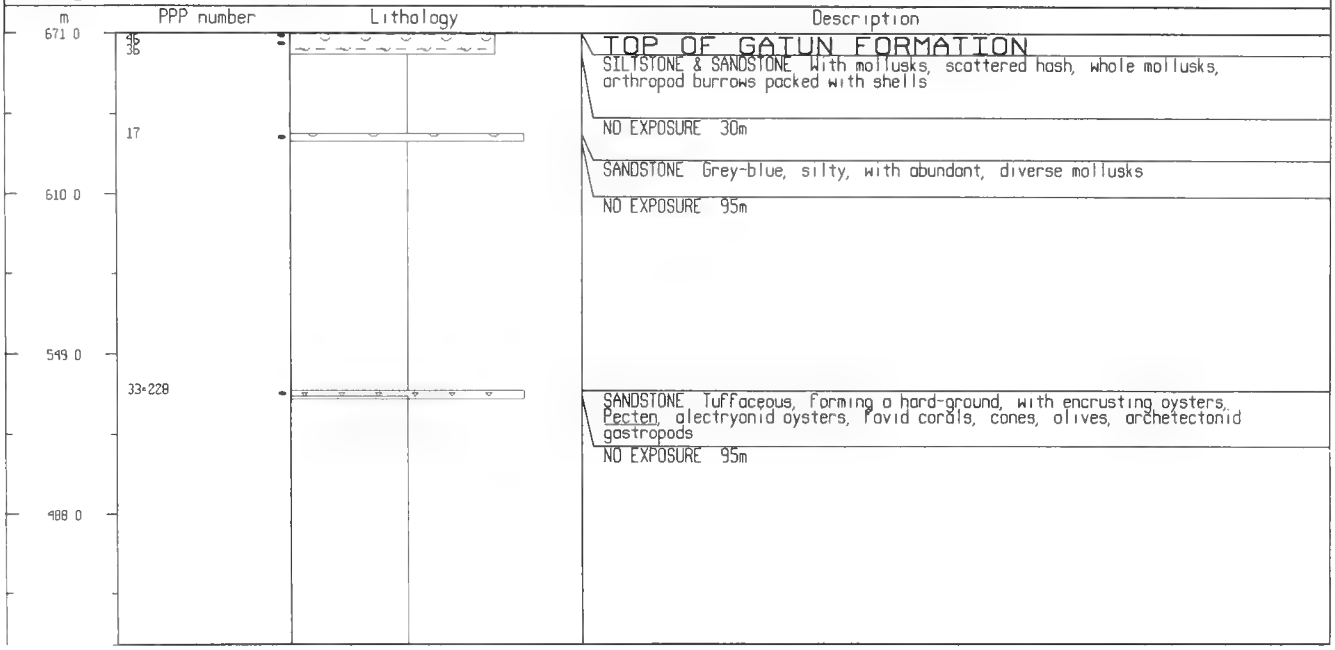
BASE OF GATUN FORMATION

BASEMENT Cretaceous volcanics

PANAMA CANAL BASIN

Section 2

Margarita to Gatun



TOP OF GATUN FORMATION

SILTSTONE & SANDSTONE With mollusks, scattered hash, whole mollusks, arthropod burrows packed with shells

NO EXPOSURE 30m

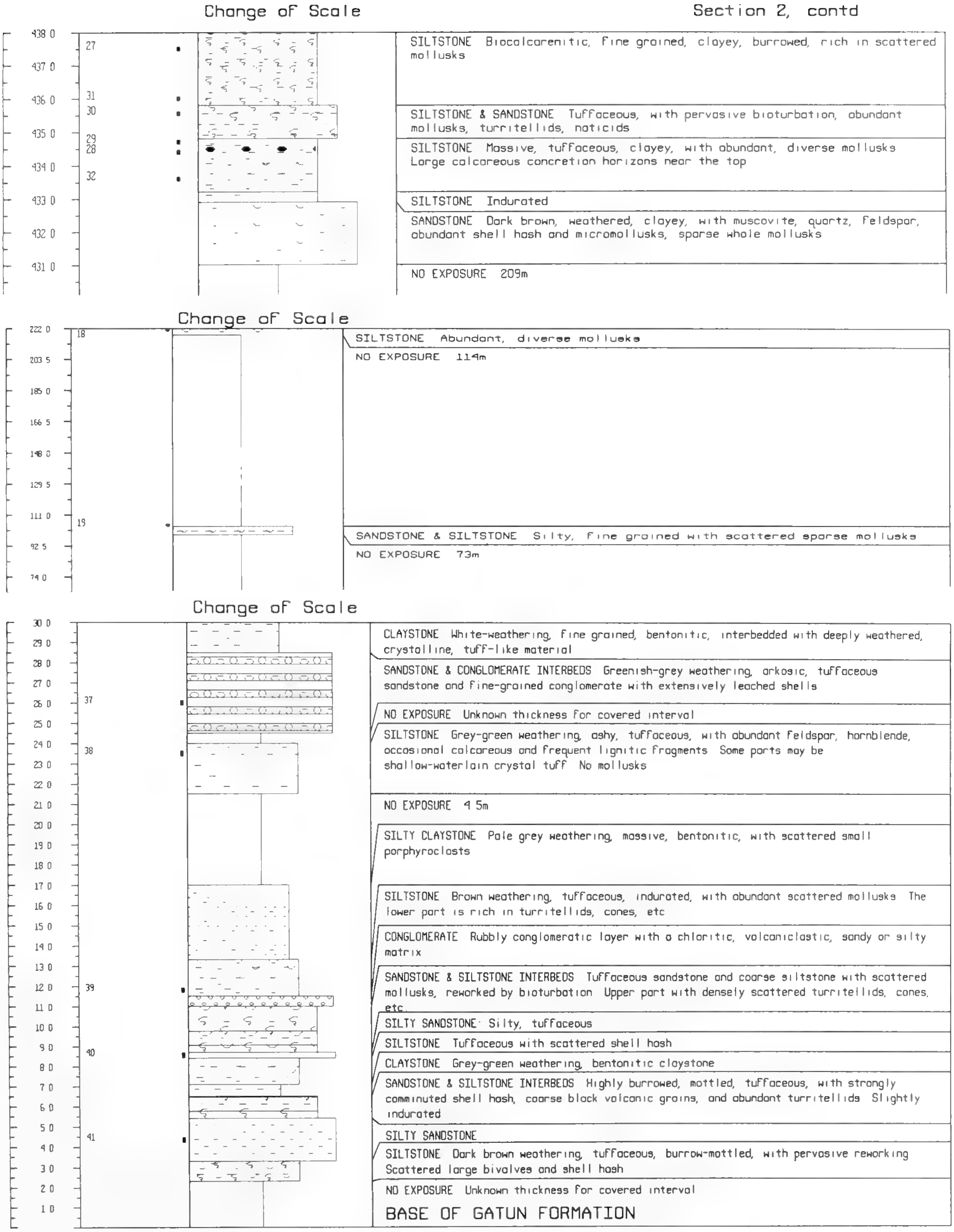
SANDSTONE Grey-blue, silty, with abundant, diverse mollusks

NO EXPOSURE 95m

SANDSTONE Tuffaceous, forming a hard-ground, with encrusting oysters, *Pecten*, alectryonid oysters, favid corals, cones, olives, archetectonid gastropods

NO EXPOSURE 95m

## Section 2, contd



SILTSTONE Biocalcarenitic, fine grained, clayey, burrowed, rich in scattered mollusks

SILTSTONE & SANDSTONE Tuffaceous, with pervasive bioturbation, abundant mollusks, turritellids, naticids

SILTSTONE Massive, tuffaceous, clayey, with abundant, diverse mollusks Large calcareous concretion horizons near the top

SILTSTONE Indurated

SANDSTONE Dark brown, weathered, clayey, with muscovite, quartz, feldspar, abundant shell hash and micromollusks, sparse whole mollusks

NO EXPOSURE 209m

SILTSTONE Abundant, diverse mollusks

NO EXPOSURE 114m

SANDSTONE & SILTSTONE Silty, fine grained with scattered sparse mollusks

NO EXPOSURE 73m

CLAYSTONE White-weathering, fine grained, bentonitic, interbedded with deeply weathered, crystalline, tuff-like material

SANDSTONE & CONGLOMERATE INTERBEDS Greenish-grey weathering, arkosic, tuffaceous sandstone and fine-grained conglomerate with extensively leached shells

NO EXPOSURE Unknown thickness for covered interval

SILTSTONE Grey-green weathering, ashy, tuffaceous, with abundant feldspar, hornblende, occasional calcareous and frequent lignitic fragments Some parts may be shallow-waterlain crystal tuff No mollusks

NO EXPOSURE 4 5m

SILTY CLAYSTONE Pale grey weathering, massive, bentonitic, with scattered small porphyroclasts

SILTSTONE Brown weathering, tuffaceous, indurated, with abundant scattered mollusks The lower part is rich in turritellids, cones, etc

CONGLOMERATE Rubbly conglomeratic layer with a chloritic, volcaniclastic, sandy or silty matrix

SANDSTONE & SILTSTONE INTERBEDS Tuffaceous sandstone and coarse siltstone with scattered mollusks, reworked by bioturbation Upper part with densely scattered turritellids, cones, etc.

SILTY SANDSTONE· Silty, tuffaceous

SILTSTONE Tuffaceous with scattered shell hash

CLAYSTONE Grey-green weathering, bentonitic claystone

SANDSTONE & SILTSTONE INTERBEDS Highly burrowed, mottled, tuffaceous, with strongly comminuted shell hash, coarse black volcanic grains, and abundant turritellids Slightly indurated

SILTY SANDSTONE

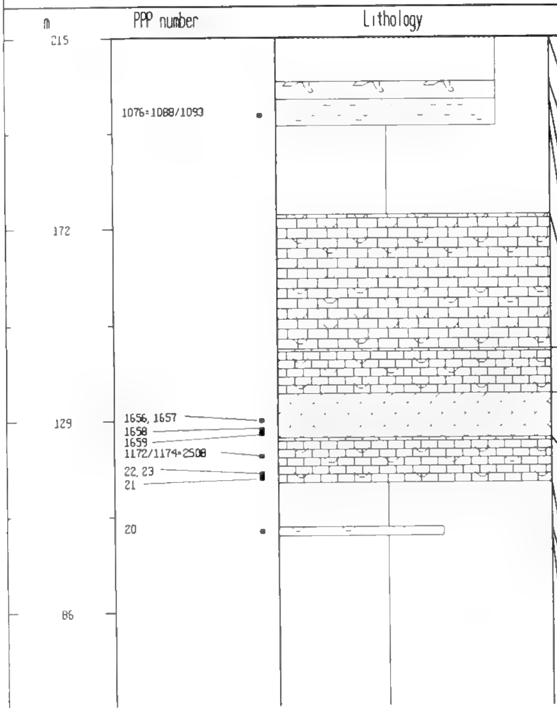
SILTSTONE Dark brown weathering, tuffaceous, burrow-mottled, with pervasive reworking Scattered large bivalves and shell hash

NO EXPOSURE Unknown thickness for covered interval

BASE OF GATUN FORMATION

PANAMA CANAL BASIN Section 3

Toro Point



Description

**SECTION AT AMBUSH ROAD**
**TOP OF CHAGRES FORMATION**

SANDSTONE Tan-weathering, massive, very thick bedded (not closely inspected-high in cliff)

SANDSTONE Tan-weathering, massive, very thick bedded (not closely inspected-high in cliff) Dense Thalassinoides burrow systems

SILTY SANDSTONE Coarse, poorly sorted, with scattered, disoriented, disarticulated bivalves and rare Strombina

NO EXPOSURE 20m

SANDY LIMESTONE Grades from unit below into alternating coquina and shelly, coarse sandstone

**TOP OF TORO MEMBER**

LIMESTONE Shelly, barnacle and echinoid coquina with coarse sandstone to grit-sized clasts and plates, white-cream ledging unit

CROSS BEDS Thin to laminated bedding has steep, prograding foresets abruptly truncated Cross beds are alternating clayey, silty sandstone, and blue-grey, shelly, barnacle coquina Beds are 2-50cm thick

LIMESTONE Shelly, barnacle and echinoid coquina with coarse sandstone to grit-sized clasts and plates, white-cream ledging unit

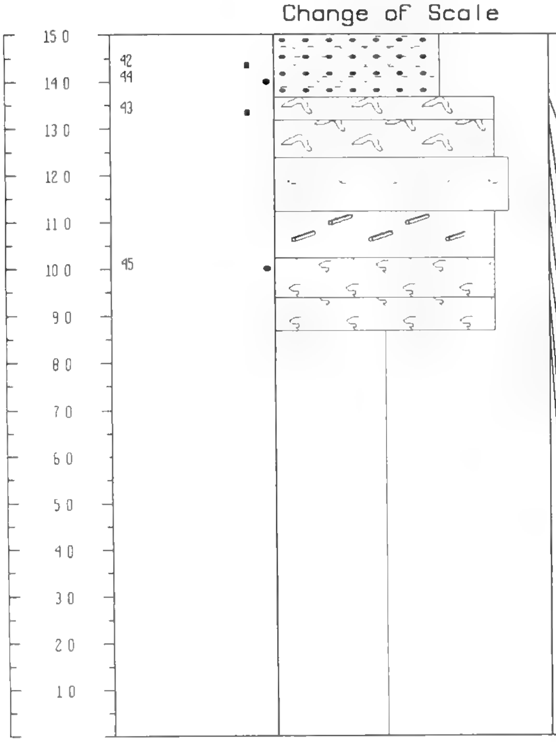
**BASE OF TORO MEMBER**
**BASE OF CHAGRES FORMATION**

NO EXPOSURE 10m

SILTSTONE Blue-grey, with scattered large mollusks

**TOP OF GATUN FORMATION.**

NO EXPOSURE 87 25m



SANDY SILTSTONE. Conglomeratic, massive, unbedded, tuffaceous, with abundant shell hash and oysters, Turritella very common

**SECTION BELOW GATUN DAM**
**HYDROELECTRIC PLANT.**

SANDSTONE Highly arkosic, tuffaceous Pervaded with callianassid burrows which contain volcanic pebbles Calcified, scattered large flat mounds (> 1m in diameter) of siderasteroid corals

SANDSTONE Green-brown weathering, tuffaceous, with scattered volcanic pebbles and large, widely spaced, calcified arthropod burrows containing volcanic pebbles

C SANDSTONE Massive, coarse, arkosic, quartzose, tuffaceous Occasional stringers of shells Tan-brown weathering, mostly unfossiliferous

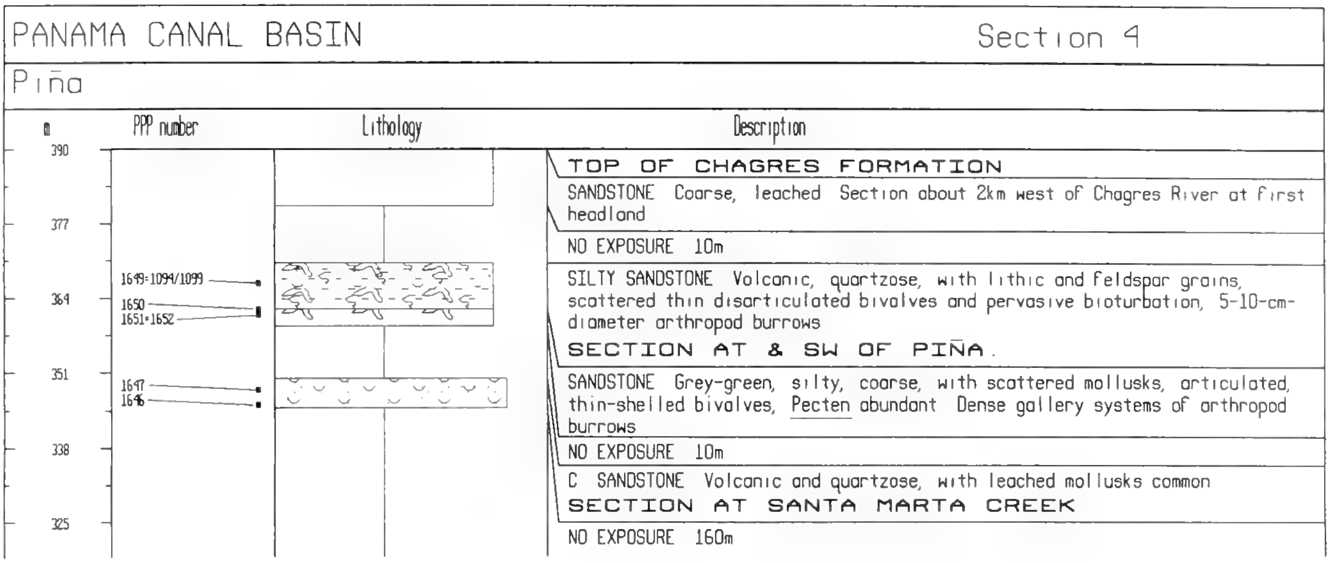
SANDSTONE Medium-grained, arkosic, tuffaceous, with scattered wood fragments and a conglomeratic base

SANDSTONE Many armoured mud or sand balls with volcanic pebbles in a fine to medium-grained, tuffaceous sandstone matrix Upper part has pervasive, small, callianassid-type burrows forming galleries Patchy, densely conglomeratic pockets in the sandstone

SANDSTONE Tuffaceous with numerous 1-cm-diameter burrows

**BASE OF GATUN FORMATION**

NO EXPOSURE Unknown thickness for covered interval



PANAMA CANAL BASIN Section 4

Piña

TOP OF CHAGRES FORMATION

SANDSTONE Coarse, leached Section about 2km west of Chagres River at first headland

NO EXPOSURE 10m

SILTY SANDSTONE Volcanic, quartzose, with lithic and feldspar grains, scattered thin disarticulated bivalves and pervasive bioturbation, 5-10-cm-diameter arthropod burrows

SECTION AT & SW OF PIÑA.

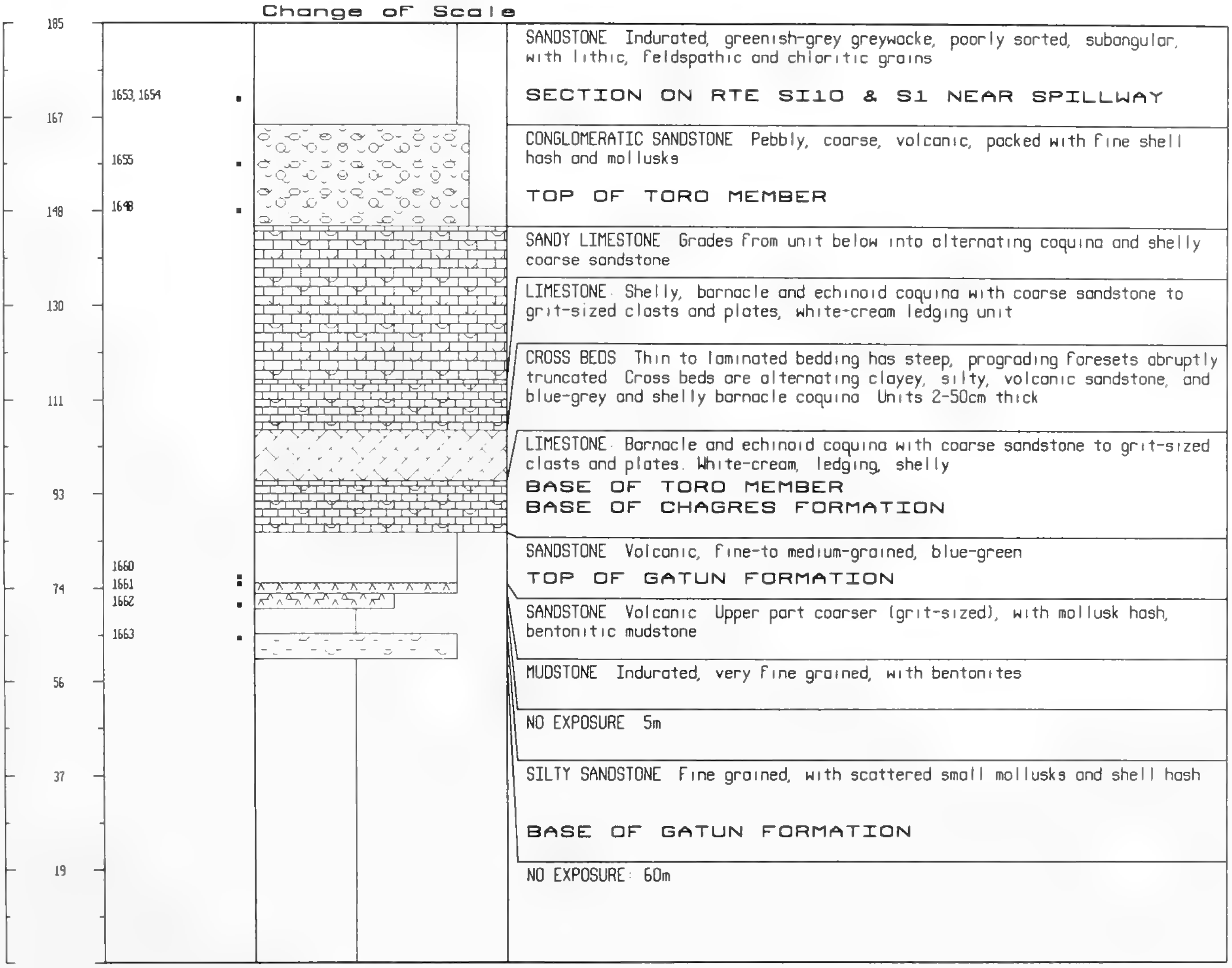
SANDSTONE Grey-green, silty, coarse, with scattered mollusks, articulated, thin-shelled bivalves, Pecten abundant Dense gallery systems of arthropod burrows

NO EXPOSURE 10m

C SANDSTONE Volcanic and quartzose, with leached mollusks common

SECTION AT SANTA MARTA CREEK

NO EXPOSURE 160m



SANDSTONE Indurated, greenish-grey greywacke, poorly sorted, subangular, with lithic, feldspathic and chloritic grains

SECTION ON RTE SI10 & S1 NEAR SPILLWAY

CONGLOMERATIC SANDSTONE Pebbly, coarse, volcanic, packed with fine shell hash and mollusks

TOP OF TORO MEMBER

SANDY LIMESTONE Grades from unit below into alternating coquina and shelly coarse sandstone

LIMESTONE Shelly, barnacle and echinoid coquina with coarse sandstone to grit-sized clasts and plates, white-cream ledging unit

CROSS BEDS Thin to laminated bedding has steep, prograding foresets abruptly truncated Cross beds are alternating clayey, silty, volcanic sandstone, and blue-grey and shelly barnacle coquina Units 2-50cm thick

LIMESTONE Barnacle and echinoid coquina with coarse sandstone to grit-sized clasts and plates. White-cream, ledging, shelly

BASE OF TORO MEMBER

BASE OF CHAGRES FORMATION

SANDSTONE Volcanic, fine-to medium-grained, blue-green

TOP OF GATUN FORMATION

SANDSTONE Volcanic Upper part coarser (grit-sized), with mollusk hash, bentonitic mudstone

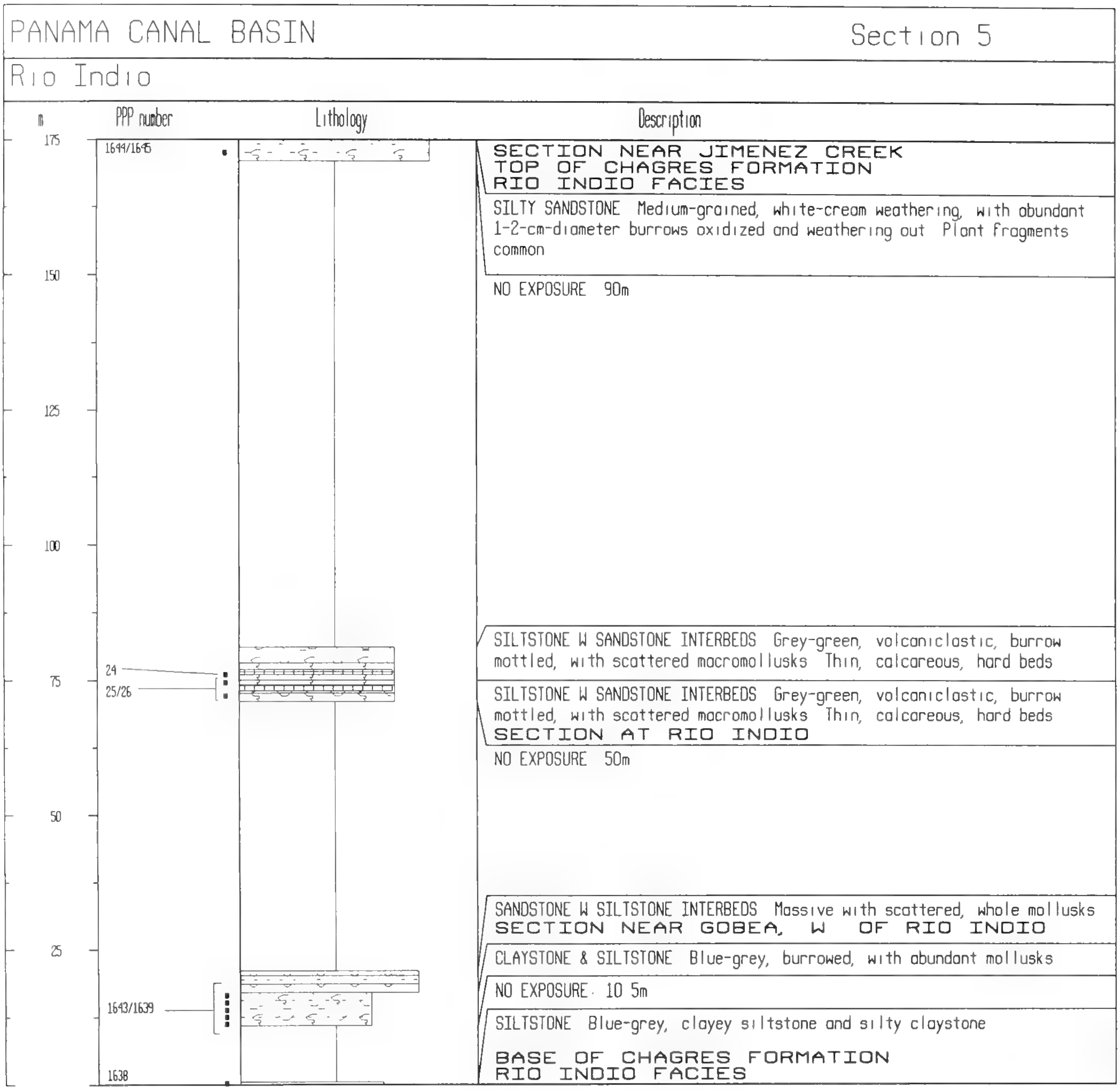
MUDSTONE Indurated, very fine grained, with bentonites

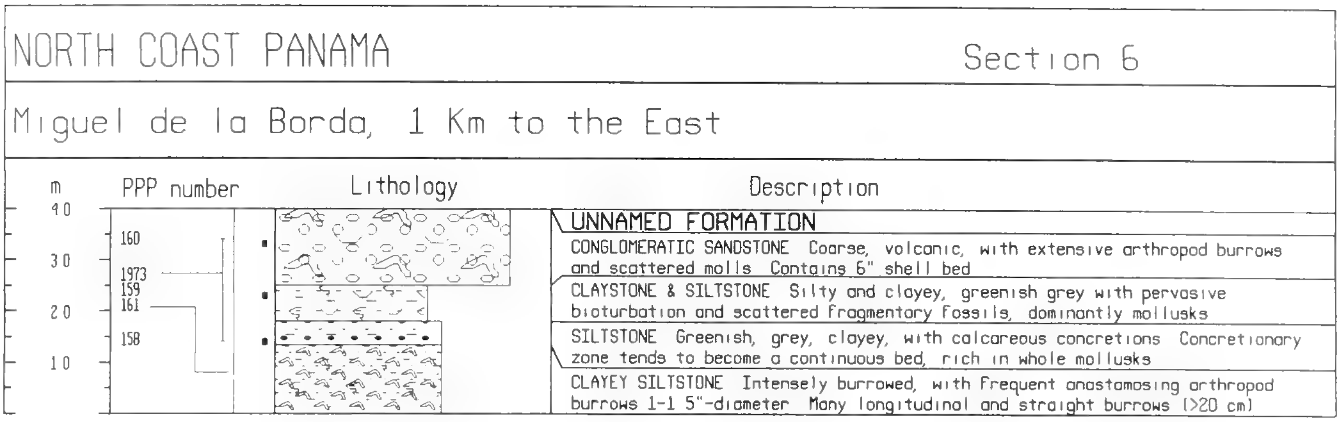
NO EXPOSURE 5m

SILTY SANDSTONE Fine grained, with scattered small mollusks and shell hash

BASE OF GATUN FORMATION

NO EXPOSURE 60m


PANAMA CANAL BASIN
Section 5
Rio Indio
m
PPP number
Lithology
Description
175
150
125
100
75
50
25
1644/1645
24
25/26
1643/1639
1638
SECTION NEAR JIMENEZ CREEK
TOP OF CHAGRES FORMATION
RIO INDIO FACIES
SILTY SANDSTONE Medium-grained, white-cream weathering, with abundant 1-2-cm-diameter burrows oxidized and weathering out Plant fragments common
NO EXPOSURE 90m
SILTSTONE W SANDSTONE INTERBEDS Grey-green, volcaniclastic, burrow mottled, with scattered macromollusks Thin, calcareous, hard beds
SILTSTONE W SANDSTONE INTERBEDS Grey-green, volcaniclastic, burrow mottled, with scattered macromollusks Thin, calcareous, hard beds
SECTION AT RIO INDIO
NO EXPOSURE 50m
SANDSTONE W SILTSTONE INTERBEDS Massive with scattered, whole mollusks
SECTION NEAR GOBEA, W OF RIO INDIO
CLAYSTONE & SILTSTONE Blue-grey, burrowed, with abundant mollusks
NO EXPOSURE 10.5m
SILTSTONE Blue-grey, clayey siltstone and silty claystone
BASE OF CHAGRES FORMATION
RIO INDIO FACIES



NORTH COAST PANAMA Section 6

Miguel de la Borda, 1 Km to the East

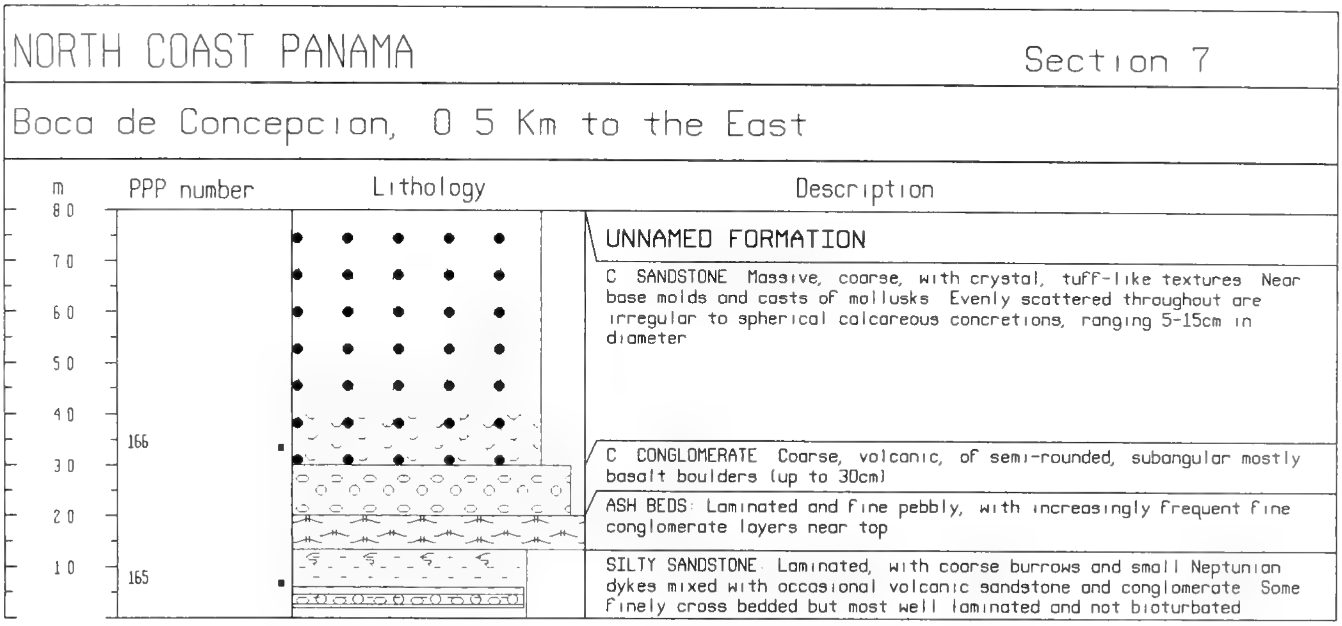
UNNAMED FORMATION

CONGLOMERATIC SANDSTONE Coarse, volcanic, with extensive arthropod burrows and scattered molls Contains 6" shell bed

CLAYSTONE & SILTSTONE Silty and clayey, greenish grey with pervasive bioturbation and scattered fragmentary fossils, dominantly mollusks

SILTSTONE Greenish, grey, clayey, with calcareous concretions Concretionary zone tends to become a continuous bed, rich in whole mollusks

CLAYEY SILTSTONE Intensely burrowed, with frequent anastomosing arthropod burrows 1-1 5"-diameter Many longitudinal and straight burrows (>20 cm)



NORTH COAST PANAMA Section 7

Boca de Concepcion, 0 5 Km to the East

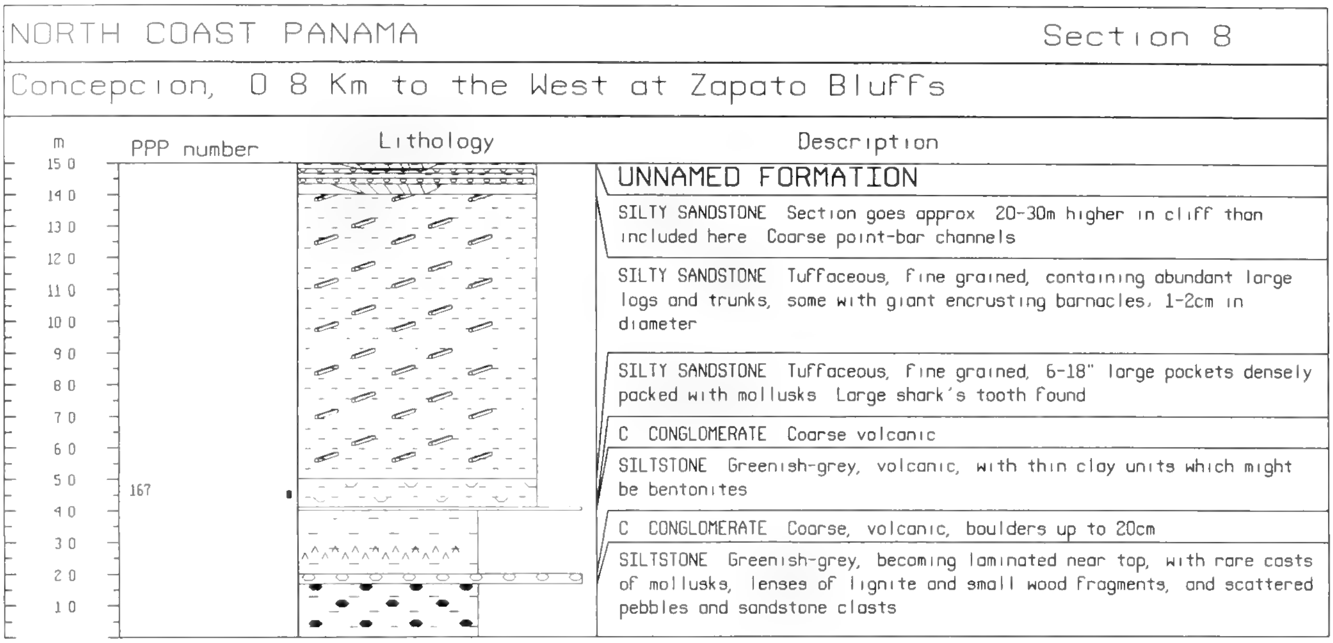
UNNAMED FORMATION

C SANDSTONE Massive, coarse, with crystal, tuff-like textures Near base molds and casts of mollusks Evenly scattered throughout are irregular to spherical calcareous concretions, ranging 5-15cm in diameter

C CONGLOMERATE Coarse, volcanic, of semi-rounded, subangular mostly basalt boulders (up to 30cm)

ASH BEDS: Laminated and fine pebbly, with increasingly frequent fine conglomerate layers near top

SILTY SANDSTONE Laminated, with coarse burrows and small Neptunian dykes mixed with occasional volcanic sandstone and conglomerate Some finely cross bedded but most well laminated and not bioturbated


NORTH COAST PANAMA Section 8

Concepcion, 0 8 Km to the West at Zapato Bluffs

UNNAMED FORMATION

SILTY SANDSTONE Section goes approx 20-30m higher in cliff than included here Coarse point-bar channels

SILTY SANDSTONE Tuffaceous, fine grained, containing abundant large logs and trunks, some with giant encrusting barnacles, 1-2cm in diameter

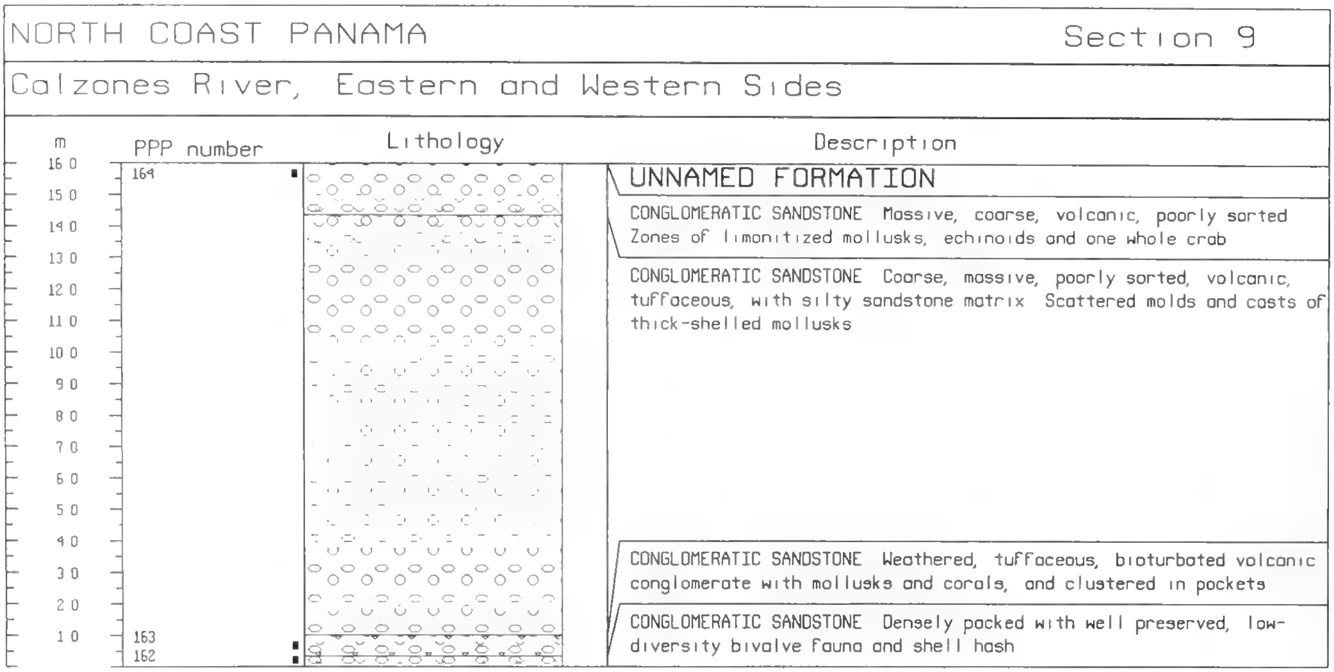
SILTY SANDSTONE Tuffaceous, fine grained, 6-18" large pockets densely packed with mollusks Large shark's tooth found

C CONGLOMERATE Coarse volcanic

SILTSTONE Greenish-grey, volcanic, with thin clay units which might be bentonites

C CONGLOMERATE Coarse, volcanic, boulders up to 20cm

SILTSTONE Greenish-grey, becoming laminated near top, with rare casts of mollusks, lenses of lignite and small wood fragments, and scattered pebbles and sandstone clasts


NORTH COAST PANAMA Section 9

Calzones River, Eastern and Western Sides

UNNAMED FORMATION

CONGLOMERATIC SANDSTONE Massive, coarse, volcanic, poorly sorted Zones of limonitized mollusks, echinoids and one whole crab

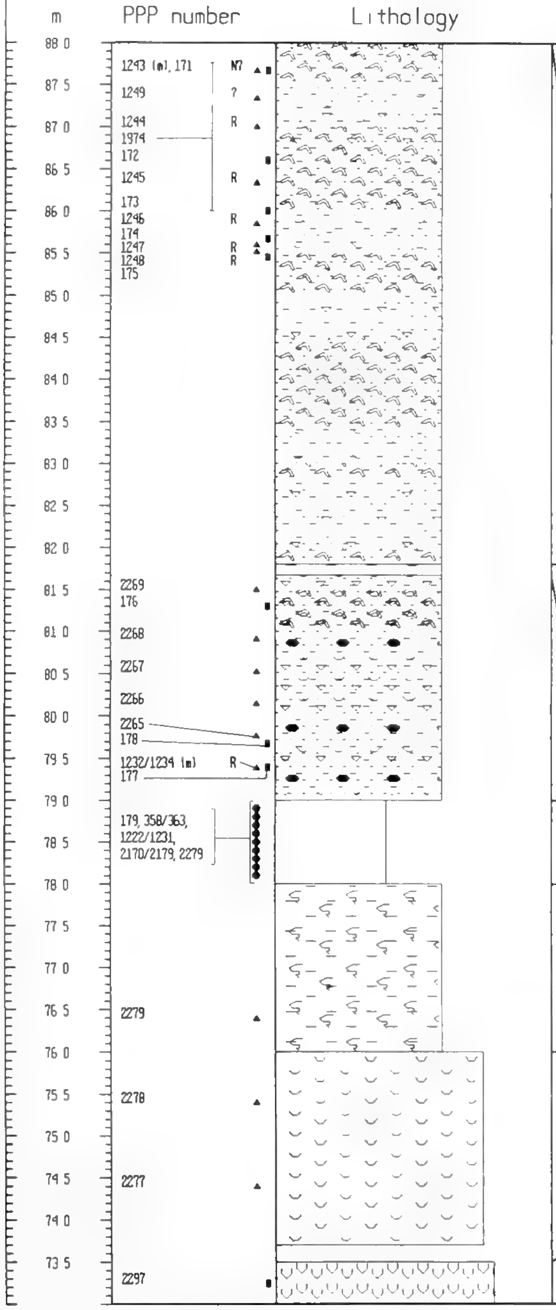
CONGLOMERATIC SANDSTONE Coarse, massive, poorly sorted, volcanic, tuffaceous, with silty sandstone matrix Scattered molds and casts of thick-shelled mollusks

CONGLOMERATIC SANDSTONE Weathered, tuffaceous, bioturbated volcanic conglomerate with mollusks and corals, and clustered in pockets

CONGLOMERATIC SANDSTONE Densely packed with well preserved, low-diversity bivalve fauna and shell hash

## BOCAS DEL TORO BASIN Section 10

### Escudo de Veraguas, Northern Coast



Description

SECTION ON W. COAST IMMEDIATELY SOUTH OF LONG BAY POINT

CLAYEY SILTSTONE Blue-grey, pale, tan-weathering, silty clay Intensely and distinctly burrowed Mostly callianassid-type fauna similar to, but much sparser than, PPP 168 Mollusks are diverse, but fragments are a greater percentage relative to whole than in PPP 168 Thin-shelled, fragile, spatangoid? echinoids are very common, but corals are mostly absent Logs are rare or few

TOP OF ESCUDO DE VERAGUAS FORMATION

SILTSTONE Marker horizons are distinctively weathering, slightly more massive units, blocky Appear to be indurated relative to burrowed zones, possibly minor disconformities

CLAYEY SILTSTONE Grey-bluish, with diverse mollusk fauna and a very common cornute coral Also common is a large pteropod, Cavolina Lines of irregular calcareous concretions and indurated arthropod burrows are typical No echinoids or logs

NO EXPOSURE Small but unknown thickness of section not exposed Sample numbers come from exposures along western part of North coast and are estimated to fall within this zone

SILTSTONE Bioclastic, clayey, sandy, with pronounced 10-cm-thick burrow zones at top

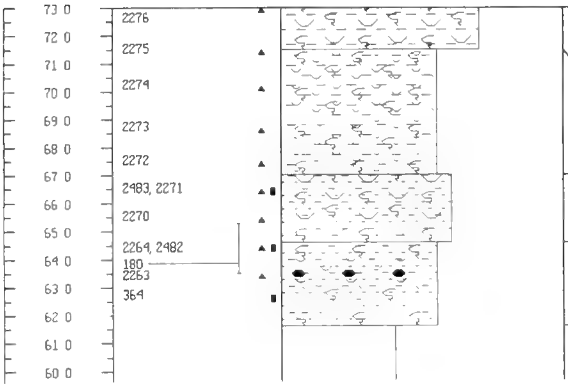
F SANDSTONE Silty, bioclastic, with diverse mollusks, scattered and disoriented, and Cupuladrians

SECTION BELOW IS 1.3 KM TO EAST ALONG NORTH COAST, ON EAST SIDE OF BREACH IN REEF AND IS EXTRAPOLATED TO LIE BELOW WEST COAST SEQUENCE.

CORAL THICKET· Coral biostrome with slender branching corals, Madracis?, Stylophora?, mussid, sand dollars, mollusks

Change of Scale

Section 10, contd



SILTSTONE & SANDSTONE Blue-grey, clayey, with fine shell hash, pervasive bioturbation

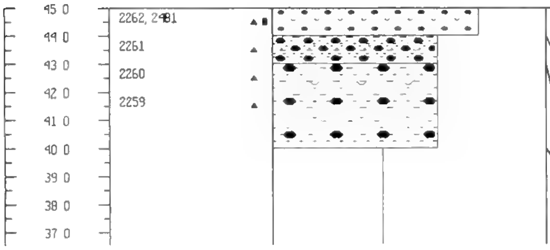
MUDSTONE Silty, bioclastic, grey, with scattered mollusks, pervasive bioturbation, fine hash

CLAYEY SILTSTONE Massive, grey, with scattered mollusks, black, larger basalt grains, pervasive bioturbation

SILTY CLAYSTONE grey-blue, massive, with pervasive bioturbation, abundant, small, thin-shelled mollusks, tellinids, pteropods

NO EXPOSURE 16 5m

Change of Scale



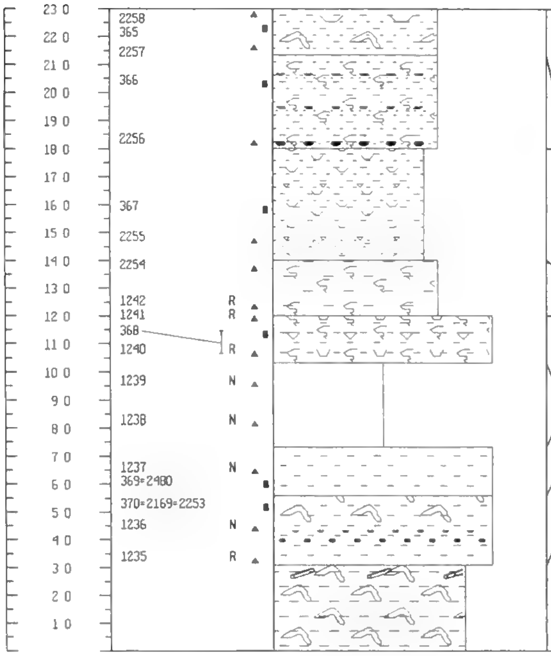
F SANDSTONE Silty, clayey, with scattered diverse mollusks, pervasive bioturbation, regular horizons of large, irregular concretions

CLAYEY SILTSTONE Blue-grey, with occasional shell fragments, regular horizons of small concretions

CLAYEY SILTSTONE Grey-blue, with regular, subcontinuos concretion horizons, few shells and very sparse shell hash

NO EXPOSURE

Change of Scale



CLAYEY SILTSTONE massive, khaki weathering, blue-grey when fresh, pervasively bioturbated Rich in very small mollusks, often densely aggregated in arthropod burrows Common strombids, rather larger gastropods, and thin-shelled, delicate bivalves

CLAYEY SILTSTONE grey-blue, with regular horizons of branching arthropod galleries, massive, bioturbated, with few whole mollusks, scattered fine hash

SILTY CLAYSTONE grey-blue, with irregular concretions, scattered small, solitary corals and rarer larger mollusks, rich in shelly hash and small mollusks

SILTSTONE Clayey, grey-blue, burrow mottled, with scattered mollusks, pervasive bioturbation

SILTY SANDSTONE tan weathering, fine grained, massive, with pervasive bioturbation, all fossils randomly oriented, abundant horn corals, diverse mollusks

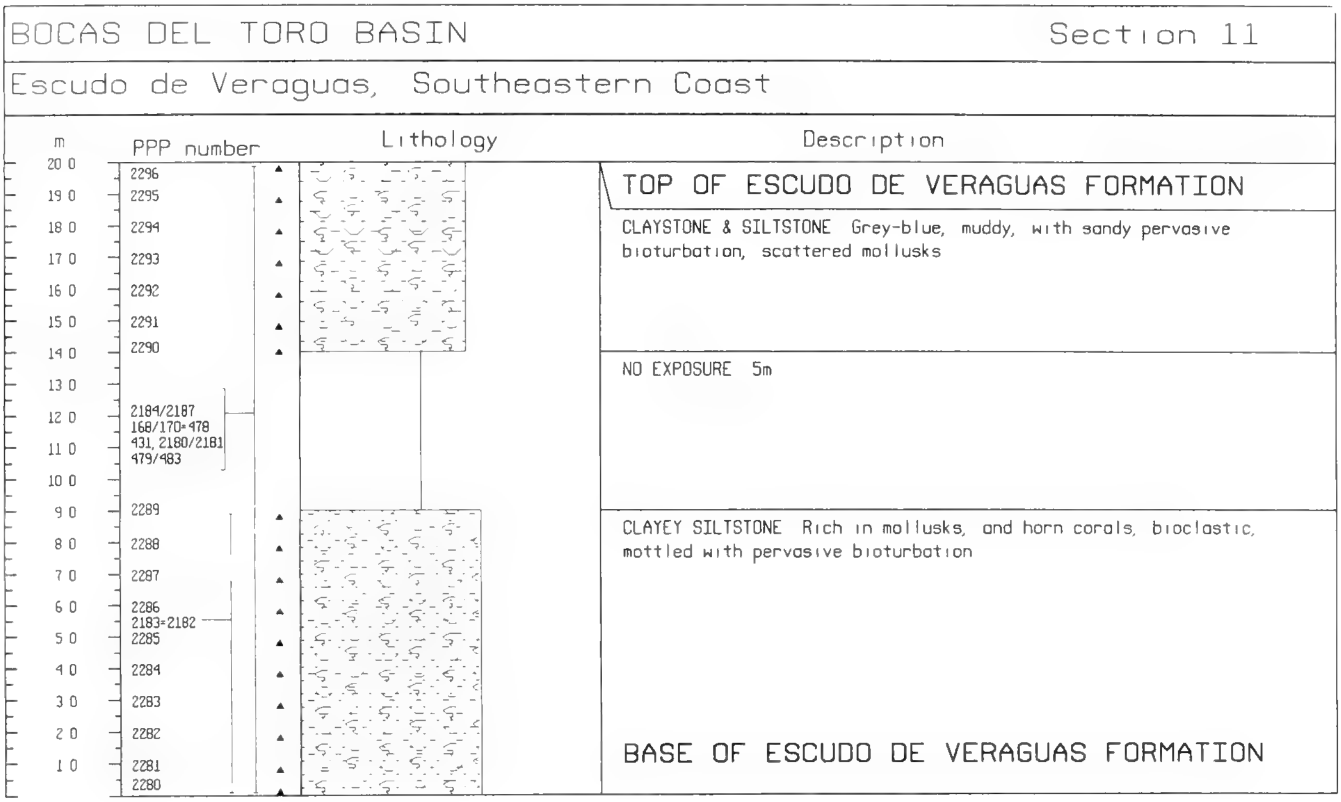
NO EXPOSURE 2-3m.

SILTY SANDSTONE light grey, and clayey siltstone, with concretions rare or absent

SILTY SANDSTONE Light grey, fine grained, and clayey siltstone, with spherical concretions and occasional whole mollusks Upper zone of irregular concretions and thalassinoid-type burrows

SANDSTONE & SILTSTONE khaki weathering, massive, shelly and fine grained with large logs and rare, whole mollusks Pervasive *Thalassinoides* burrows Note This forms N point of central north coast of Escudo

BASE OF ESCUDO DE VERAGUAS FORMATION



BOCAS DEL TORO BASIN Section 11

Escudo de Veraguas, Southeastern Coast

TOP OF ESCUDO DE VERAGUAS FORMATION

CLAYSTONE & SILTSTONE Grey-blue, muddy, with sandy pervasive bioturbation, scattered mollusks

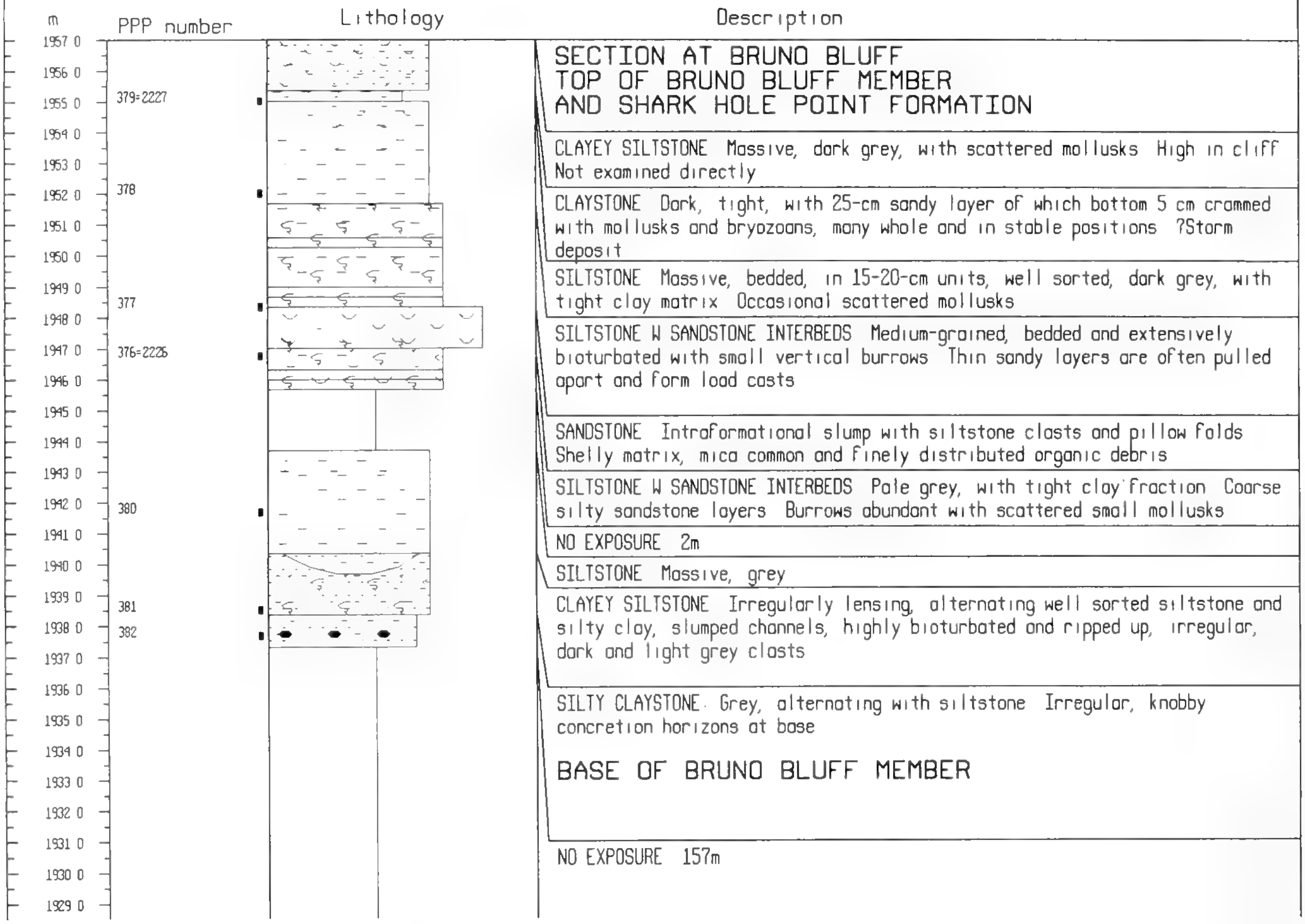
NO EXPOSURE 5m

CLAYEY SILTSTONE Rich in mollusks, and horn corals, bioclastic, mottled with pervasive bioturbation

BASE OF ESCUDO DE VERAGUAS FORMATION

## BOCAS DEL TORO BASIN Section 12

### Valiente Peninsula, Bruno Bluff to Plantain Cays



SECTION AT BRUNO BLUFF
TOP OF BRUNO BLUFF MEMBER
AND SHARK HOLE POINT FORMATION

CLAYEY SILTSTONE Massive, dark grey, with scattered mollusks High in cliff Not examined directly

CLAYSTONE Dark, tight, with 25-cm sandy layer of which bottom 5 cm crammed with mollusks and bryozoans, many whole and in stable positions ?Storm deposit

SILTSTONE Massive, bedded, in 15-20-cm units, well sorted, dark grey, with tight clay matrix Occasional scattered mollusks

SILTSTONE W SANDSTONE INTERBEDS Medium-grained, bedded and extensively bioturbated with small vertical burrows Thin sandy layers are often pulled apart and form load casts

SANDSTONE Intraformational slump with siltstone clasts and pillow folds Shelly matrix, mica common and finely distributed organic debris

SILTSTONE W SANDSTONE INTERBEDS Pale grey, with tight clay fraction Coarse silty sandstone layers Burrows abundant with scattered small mollusks

NO EXPOSURE 2m

SILTSTONE Massive, grey

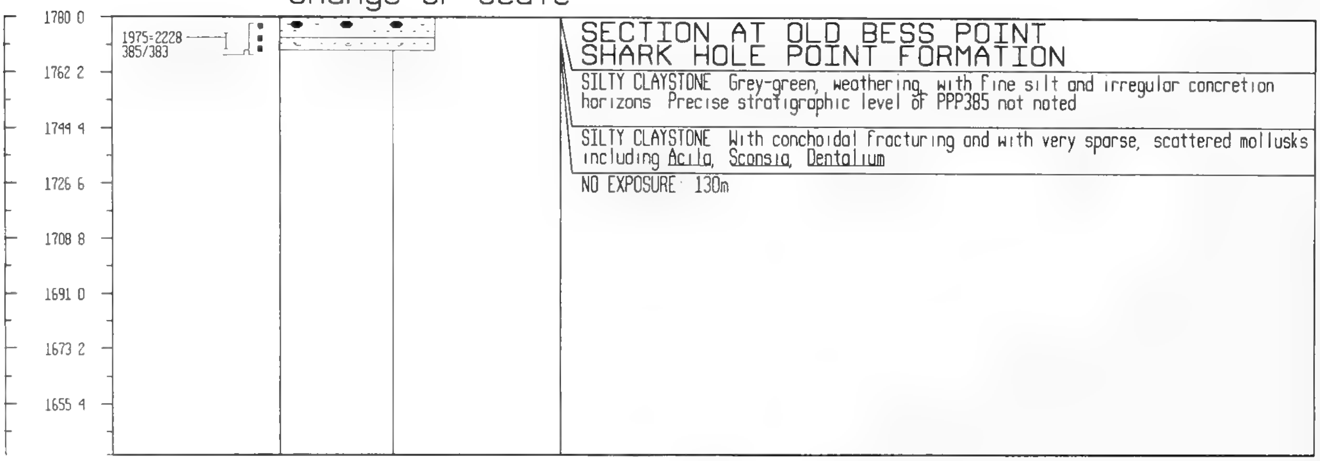
CLAYEY SILTSTONE Irregularly lensing, alternating well sorted siltstone and silty clay, slumped channels, highly bioturbated and ripped up, irregular, dark and light grey clasts

SILTY CLAYSTONE Grey, alternating with siltstone Irregular, knobby concretion horizons at base

BASE OF BRUNO BLUFF MEMBER

NO EXPOSURE 157m

Change of Scale



SECTION AT OLD BESS POINT
SHARK HOLE POINT FORMATION

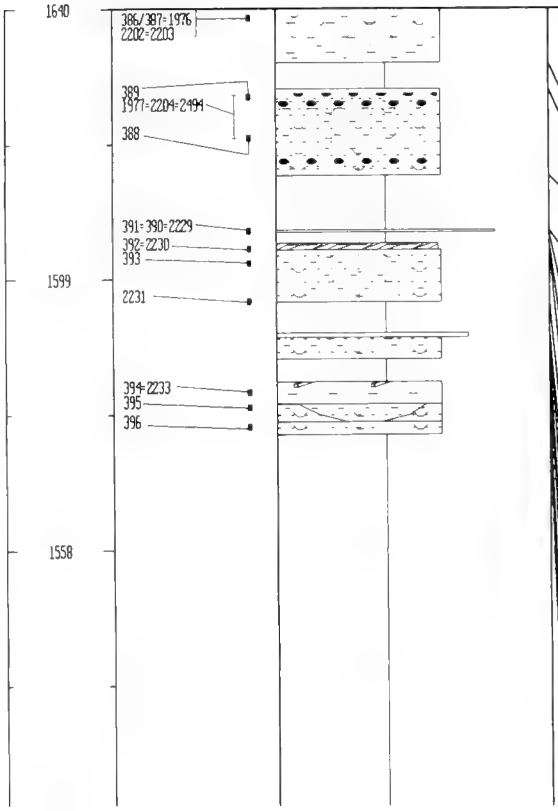
SILTY CLAYSTONE Grey-green, weathering, with fine silt and irregular concretion horizons Precise stratigraphic level of PPP385 not noted

SILTY CLAYSTONE With conchoidal fracturing and with very sparse, scattered mollusks including *Acila*, *Sconsia*, *Dentalium*

NO EXPOSURE 130m

Change of Scale

Section 12, contd



SILTSTONE Massive, fine, dark grey, with tight clay matrix, sporadic large Dentalium and other snails, uncommon bivalves

SECTION AT SHARK HOLE POINT

NO EXPOSURE 4m

CLAYEY SILTSTONE Dark grey, massive, finely micaceous, tight, with scattered mollusks Prominent concretionary horizon near the base

BASE OF SHARK HOLE POINT FORMATION

NO EXPOSURE 8 33m

TOP OF NANCY POINT FORMATION

SANDSTONE Possibly lensing, rich shell bed

NO EXPOSURE 1 66m

CROSS BEDDED SILTSTONE Micaceous, green, laminated, scoured and cross bedded

CLAYEY SILTSTONE Massive, chippy, green-weathering, grey-blue, tight Scattered mollusks, including Dentalium

NO EXPOSURE 4 66m

SANDSTONE & SILTSTONE Laminated, greenish

CLAYEY SILTSTONE Sparsely fossiliferous, massive, micaceous Dentalium common and other mollusks sporadic

NO EXPOSURE 3 33m

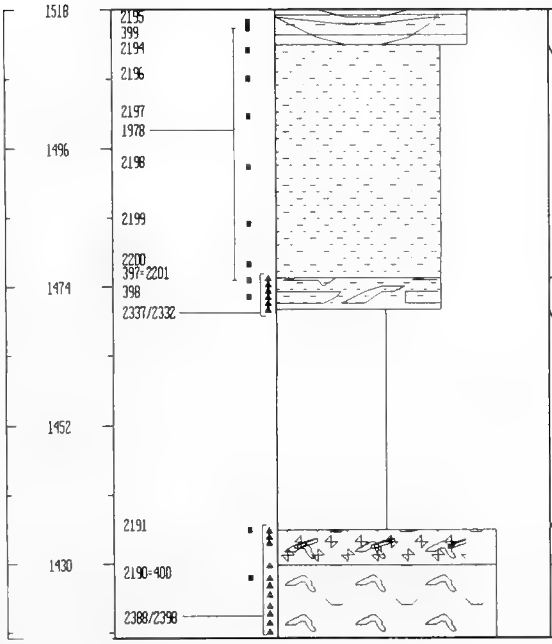
SILTSTONE Fine grained, massive, brown weathering, micaceous, and dark blue claystone Lignitized log fragments 3' long to 6" maximum diameter

CLAYEY SILTSTONE Massive, micaceous, with lenses and scattered mollusks

CLAYEY SILTSTONE Massive, micaceous, with scattered mollusks

NO EXPOSURE 57m

Change of Scale



SANDSTONE & SILTSTONE INTERBEDS Laminated, silty clay with scattered rare mollusks Coarse volcanic sandstone channel up to 1m thick

CLAYEY SILTSTONE Micaceous, with occasional mollusks

CLAYEY SILTSTONE Grey-blue, laminated Channels with volcanic conglomeratic sandstone containing large clasts of laminated siltstone and claystone

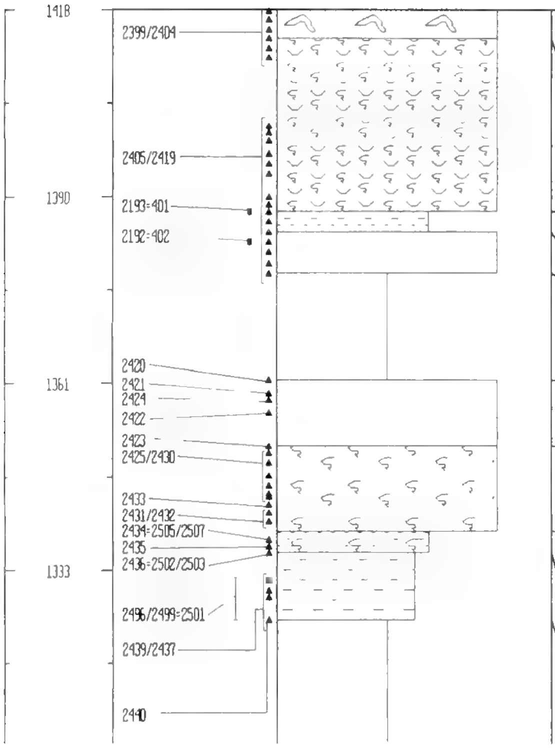
NO EXPOSURE 35m

SANDSTONE Muddy, coarse with bimodal, grain size, volcanic and calcareous grains, wood logs and fragments, pervasive bioturbation, occasional mollusks

SANDSTONE Massive, muddy, coarse, with muscovite, fine shell hash, volcanic grains, pervasive bioturbation, burrow mottling, bimodal grain size

Change of Scale

Section 12, contd



SANDSTONE Massive, muddy, coarse, with muscovite, fine shell hash, volcanic grains, pervasive bioturbation, burrow mottling, bimodal grain size

SANDSTONE Muddy, bioclastic, volcanic, with bimodal grain size, muscovite, pervasive bioturbation, occasional small mollusks, lignite, burrow mottling

SILTY MUDSTONE Packed with lignite fragments, micro mollusks

SANDSTONE Muddy, volcanic, packed with lignite fragments, micro mollusks

NO EXPOSURE 16m

SANDSTONE Muddy, greywacke

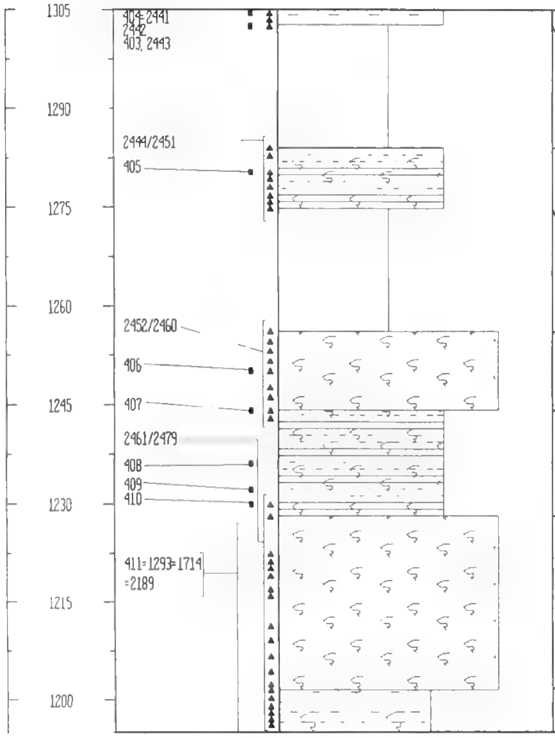
SANDSTONE Thin bedded, muddy, coarse, with bimodal grain size, basalt granules, lignite, sparse mollusks, thin silty mudstone units, burrow mottling Bioclastic

SILTY MUDSTONE Medium grained, evenly bedded, muddy sandstone and siltstone that are turbiditic?, lignitic, burrow mottled

CLAYSTONE Tight, blue, silty, with burrow fills, occasional massive coarse sandstone units

NO EXPOSURE 20m

Change of Scale



SILTSTONE Muddy, lignitic

NO EXPOSURE 18 5m

SANDSTONE & MUDSTONE Sandstone is pebbly, muddy, burrow mottled, with tubular burrows, mudstone is laminated sublenticularly, bioclastic, lignitic and micaceous

NO EXPOSURE 19m

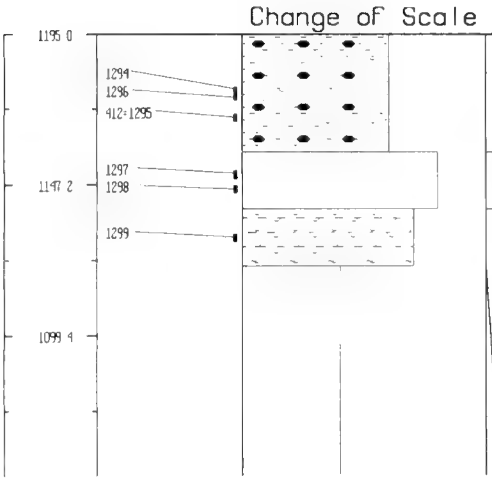
SANDSTONE Muddy, lignitic, micaceous, thick bedded, with pervasive bioturbation

SANDSTONE & MUDSTONE Clean, well bedded, burrow mottled sandstone alternating with slightly silty mudstone

SANDSTONE Muddy, burrow mottled, with volcanic granules, fine lignite, and sparse, whole mollusks

MUDSTONE & SILTSTONE Muddy, with pervasive bioturbation, common whole mollusks

## Section 12, contd



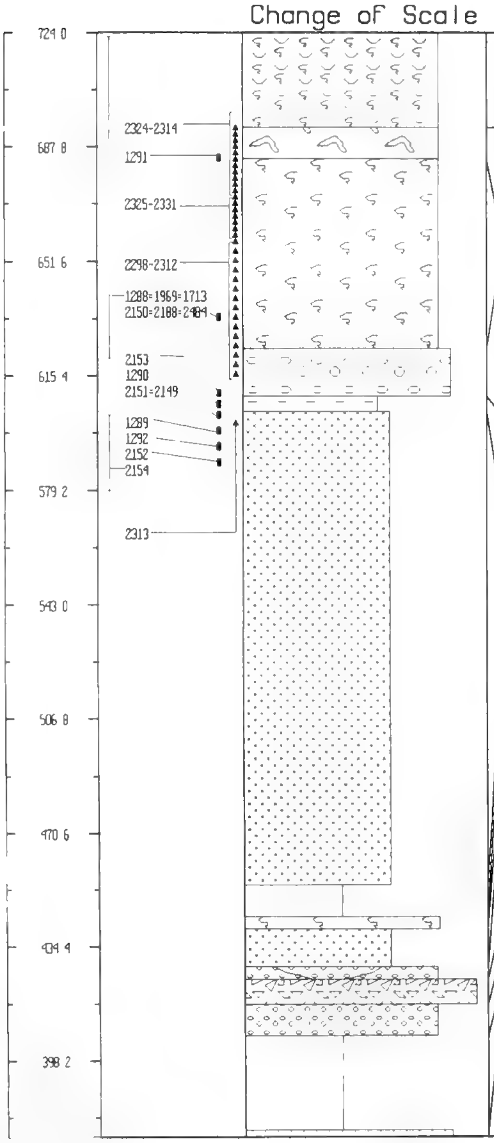
CLAYEY SILTSTONE Micaceous, dark blue Occasional coarse, volcanic sandstone channels near base Abundant shell hash and scattered mollusks Large Dentalium Slabby concretion horizons

SANDSTONE Coarse grained, thick bedded, volcanic, vaguely laminated

SANDSTONE & SILTSTONE Medium bedded, blue, coarse, quartoze, volcanic, alternating with clayey, silty sandstone and clayey siltstone, with scattered mollusks

### BASE OF NANCY POINT FORMATION

NO EXPOSURE 398m



SANDSTONE Indurated, quartoze, chippy, pervasively bioturbated, with shelly hash and scattered mollusks, that are hard to extract

### TOP OF TOBABE SANDSTONE

SANDSTONE Indurated, quartoze, chippy, pervasively bioturbated, with shelly hash and scattered mollusks, that are hard to extract Discrete thalassinoid burrows

SANDSTONE Indurated, quartoze, chippy, with uncommon mollusks and scattered, vertical, circular-diameter burrows Scattered to abundant spatangoid echinoids

CONGLOMERATIC SANDSTONE Polymict, poorly sorted and vaguely and streakily bedded, pebbly mudstone interbedded with conglomerate Clasts rounded, 10-12 cm in diameter

### BASE OF TOBABE SANDSTONE

MUDSTONE Blue-grey, infilling hummocky surface of the basalt No borings

### TOP OF UNNAMED VOLCANICS

BASALT Blue-black, massive, usually columnar

NO EXPOSURE 10m

SANDSTONE Thick-bedded alternations of coarse, volcanic boulder spreads

BASALT Columnar

CONGLOMERATE Boulder supported, with interbedded coarse sandstone lenses and stringers of boulders Clasts 6-20 cm in diameter, roughly sorted in each unit

VOLCANIC BRECCIA Basalt flow breccia

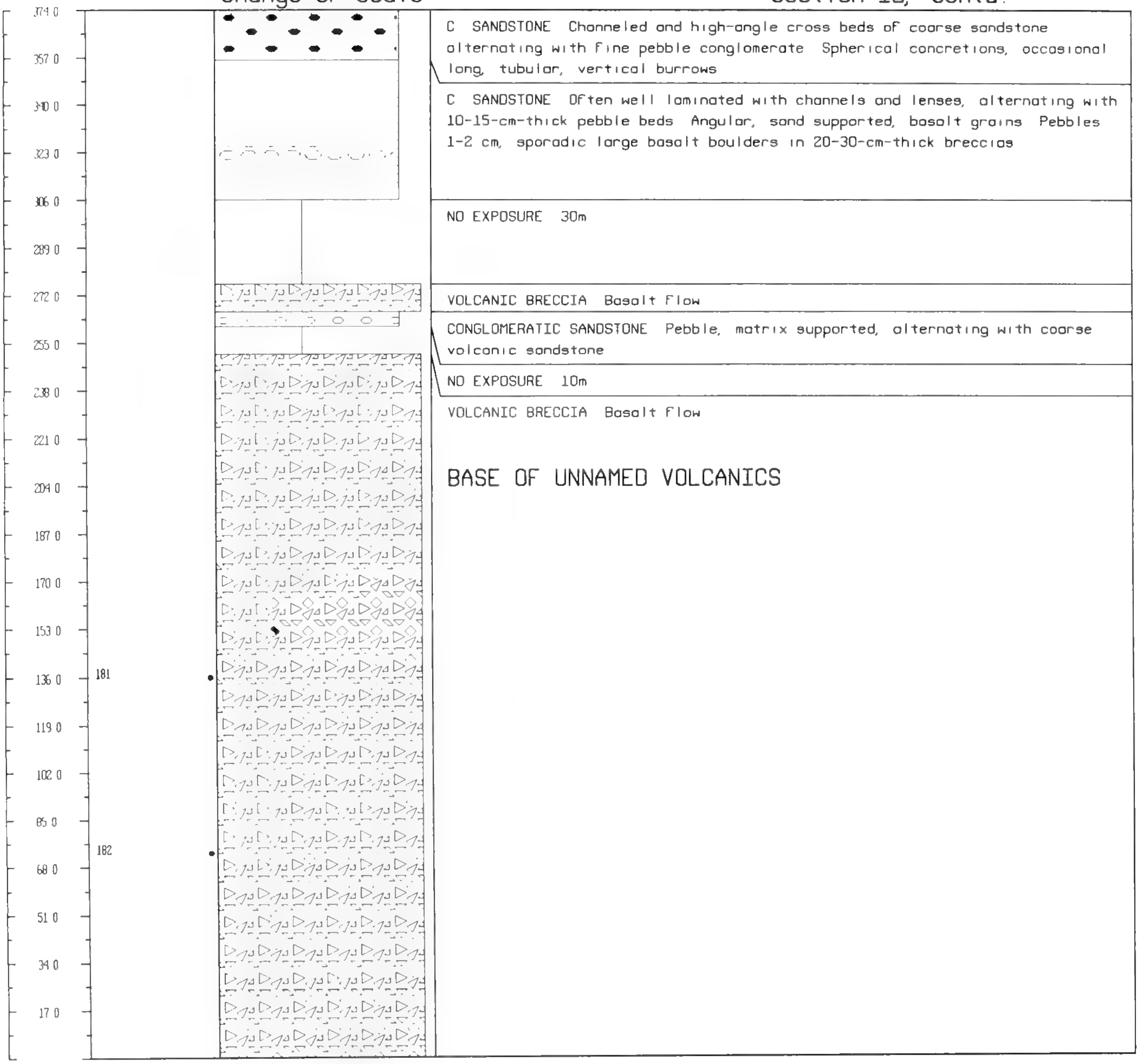
CONGLOMERATE Coarsely stratified, boulder supported, volcanic

NO EXPOSURE 30m

C SANDSTONE Channeled and high-angle cross beds of coarse sandstone alternating with fine pebble conglomerate Spherical concretions, occasional long, tubular, vertical burrows

Change of Scale

Section 12, contd.



C SANDSTONE Channeled and high-angle cross beds of coarse sandstone alternating with fine pebble conglomerate Spherical concretions, occasional long, tubular, vertical burrows

C SANDSTONE Often well laminated with channels and lenses, alternating with 10-15-cm-thick pebble beds Angular, sand supported, basalt grains Pebbles 1-2 cm, sporadic large basalt boulders in 20-30-cm-thick breccias

NO EXPOSURE 30m

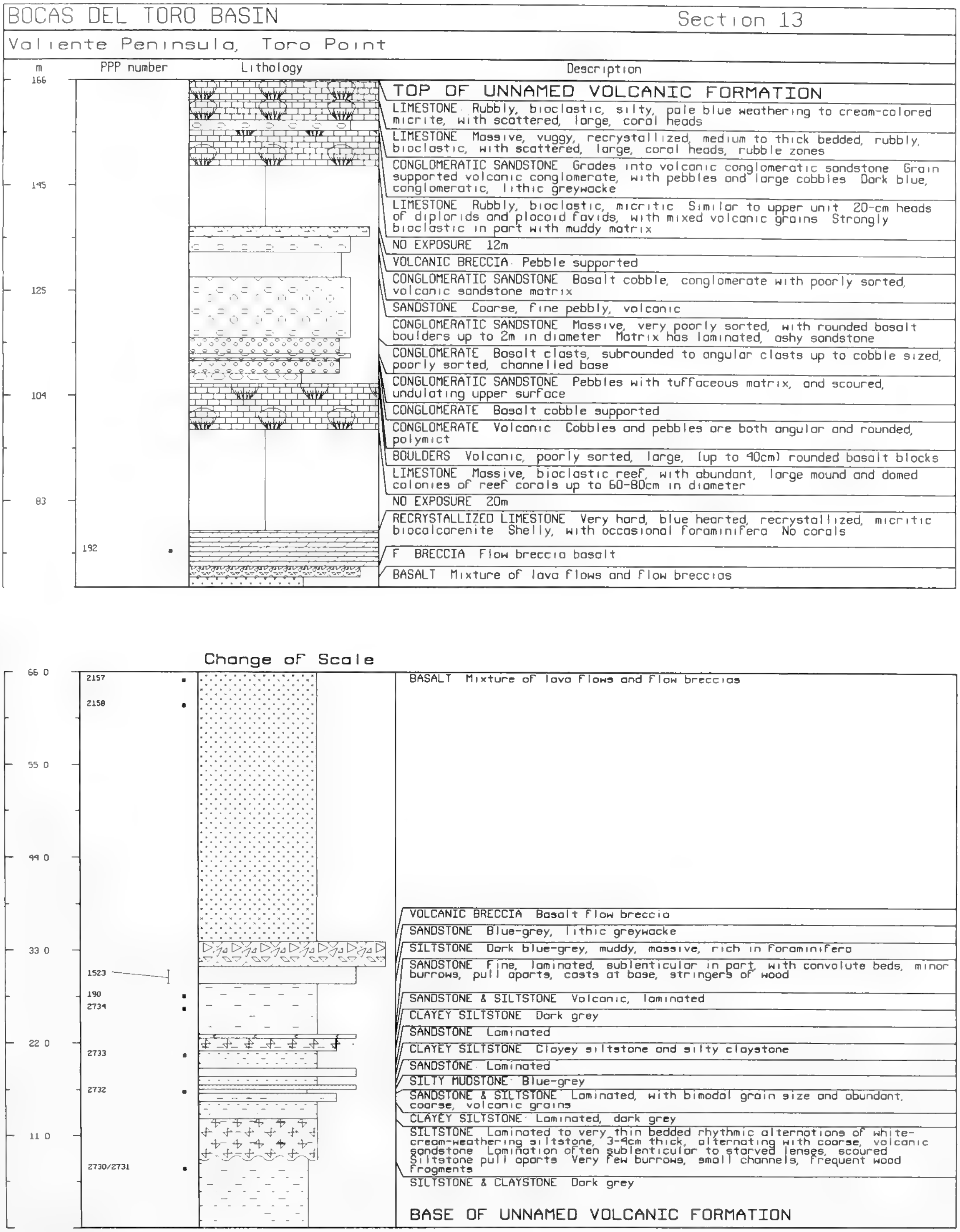
VOLCANIC BRECCIA Basalt flow

CONGLOMERATIC SANDSTONE Pebble, matrix supported, alternating with coarse volcanic sandstone

NO EXPOSURE 10m

VOLCANIC BRECCIA Basalt flow

BASE OF UNNAMED VOLCANICS



BOCAS DEL TORO BASIN Section 13

Valiente Peninsula, Toro Point

| m | PPP number | Lithology | Description |
|---|---|---|---|

TOP OF UNNAMED VOLCANIC FORMATION

LIMESTONE Rubbly, bioclastic, silty, pale blue weathering to cream-colored micrite, with scattered, large, coral heads

LIMESTONE Massive, vuggy, recrystallized, medium to thick bedded, rubbly, bioclastic, with scattered, large, coral heads, rubble zones

CONGLOMERATIC SANDSTONE Grades into volcanic conglomeratic sandstone Grain supported volcanic conglomerate, with pebbles and large cobbles Dark blue, conglomeratic, lithic greywacke

LIMESTONE Rubbly, bioclastic, micritic Similar to upper unit 20-cm heads of diplorids and plocoid favids, with mixed volcanic grains Strongly bioclastic in part with muddy matrix

NO EXPOSURE 12m

VOLCANIC BRECCIA Pebble supported

CONGLOMERATIC SANDSTONE Basalt cobble, conglomerate with poorly sorted, volcanic sandstone matrix

SANDSTONE Coarse, fine pebbly, volcanic

CONGLOMERATIC SANDSTONE Massive, very poorly sorted, with rounded basalt boulders up to 2m in diameter Matrix has laminated, ashy sandstone

CONGLOMERATE Basalt clasts, subrounded to angular clasts up to cobble sized, poorly sorted, channelled base

CONGLOMERATIC SANDSTONE Pebbles with tuffaceous matrix, and scoured, undulating upper surface

CONGLOMERATE Basalt cobble supported

CONGLOMERATE Volcanic Cobbles and pebbles are both angular and rounded, polymict

BOULDERS Volcanic, poorly sorted, large, (up to 40cm) rounded basalt blocks

LIMESTONE Massive, bioclastic reef, with abundant, large mound and domed colonies of reef corals up to 60-80cm in diameter

NO EXPOSURE 20m

RECRYSTALLIZED LIMESTONE Very hard, blue hearted, recrystallized, micritic biocalcarenite Shelly, with occasional foraminifera No corals

F BRECCIA Flow breccia basalt

BASALT Mixture of lava flows and flow breccias

Change of Scale

BASALT Mixture of lava flows and flow breccias

VOLCANIC BRECCIA Basalt flow breccia

SANDSTONE Blue-grey, lithic greywacke

SILTSTONE Dark blue-grey, muddy, massive, rich in foraminifera

SANDSTONE Fine, laminated, sublenticular in part, with convolute beds, minor burrows, pull aparts, casts at base, stringers of wood

SANDSTONE & SILTSTONE Volcanic, laminated

CLAYEY SILTSTONE Dark grey

SANDSTONE Laminated

CLAYEY SILTSTONE Clayey siltstone and silty claystone

SANDSTONE Laminated

SILTY MUDSTONE Blue-grey

SANDSTONE & SILTSTONE Laminated, with bimodal grain size and abundant, coarse, volcanic grains

CLAYEY SILTSTONE Laminated, dark grey

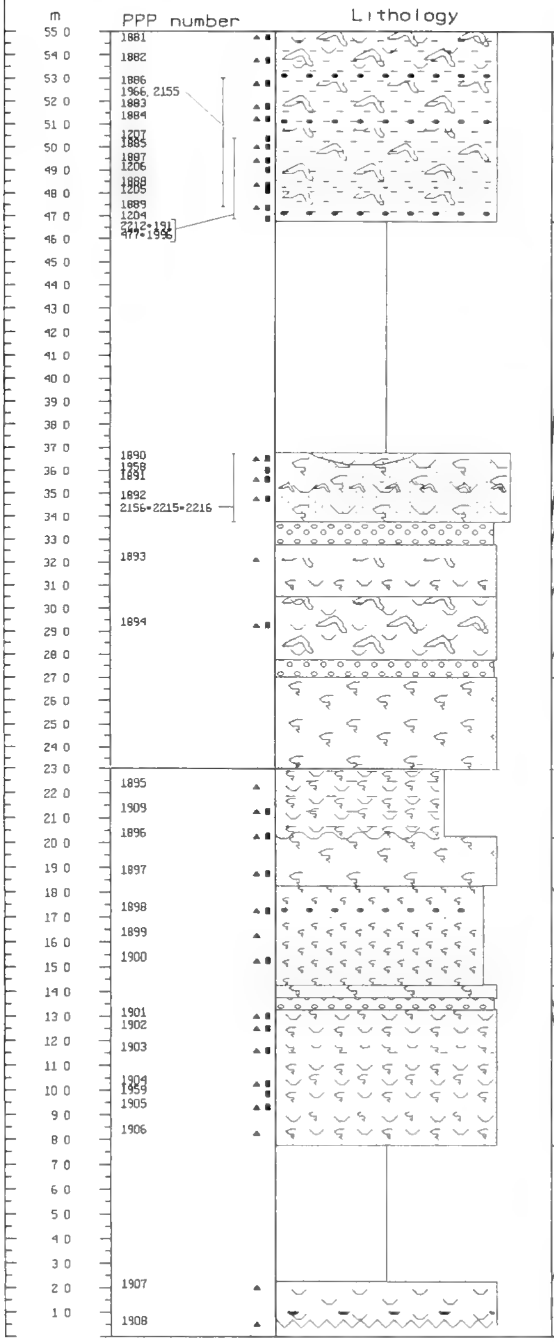
SILTSTONE Laminated to very thin bedded rhythmic alternations of white-cream-weathering siltstone, 3-4cm thick, alternating with coarse, volcanic sandstone Lamination often sublenticular to starved lenses, scoured Siltstone pull aparts Very few burrows, small channels, frequent wood fragments

SILTSTONE & CLAYSTONE Dark grey

BASE OF UNNAMED VOLCANIC FORMATION

BOCAS DEL TORO BASIN — Section 14

Valiente Peninsula, Toro Cays



Description

**FINGER ISLAND**
**NANCY POINT FORMATION**

SILTY SANDSTONE Dark blue-gray, muddy, volcanic Abundant fine shell hash, sparsely scattered, diverse mollusks Pervasive bioturbation, prominent concretion horizons and Thalassinoides burrow systems

NO EXPOSURE 10m

**TORO CAYS**
**TOBABE SANDSTONE**

C SANDSTONE Massive blue-gray, volcanic, shelly, with pervasive burrowing (tubes 1-3cm in diameter), mottling Sparsely shelly disarticulated *Pecten*, mellitid echinoids Scattered granules, pebbles of basalt, calcified burrow systems in middle 20cm Channels with coarse, laminated shelly sandstone and large rip-up clay clasts 5x30cm large shell-filled burrows (vertical) High energy, shallow, nearshore, rapidly deposited

CONGLOMERATE Volcanic, polymict, angular pebbles, mixed volcanic and carbonate, poorly sorted Clasts becoming cobbles (volcanic) at base, some thick shelled mollusks

SANDSTONE Tan weathering, volcanic, massive, with mixed volcanic and carbonate grains, pervasive burrows *Thalassinoides* system in middle of unit, 6-10-cm shell horizons in lower part Strongly ribbed, thick-shelled bivalves

SANDSTONE Grey-blue, volcanic, massive, with calcified burrow systems throughout unit, many long, straight, near-vertical tubes, sparse shells, elaborate galleries

CONGLOMERATE Volcanic, rounded cobbles, markedly coarsening upwards, mixed basalt and sediment clasts Occasional angular clasts

SANDSTONE Volcanic, massive, burrowed, with distinctive vertical joints Burrow systems not cemented and therefore not weathering out Lower 1m is a calcarenite with volcanic granules 2-3 times larger *Pecten* shell bed, with single, concave-up shells

SILTSTONE Grey-green, muddy, massive, pervasively bioturbated, burrow mottled, grey-green, forams, with fine shell hash, scattered whole mollusks, volcanic granules

SANDSTONE Volcanic Jointed rugose surface on weathered rock is very distinctive Strongly calcified, coarse, fairly clean, well sorted, burrow mottled

F SANDSTONE Blue-green, muddy, silty, massive, with pervasive burrow mottling

SANDSTONE Massive, muddy, hard, with calcareous cement, and pervasive bioturbation

CONGLOMERATE Volcanic (mixed clasts and carbonate) with subangular pebbles

SANDSTONE Green-blue, volcanic, muddy, fine to medium greywacke Pervasively bioturbated, with small burrows, sparse, fine shell hash, several small disconformities, occasional laminated bedding *Turritella* and other mollusks common

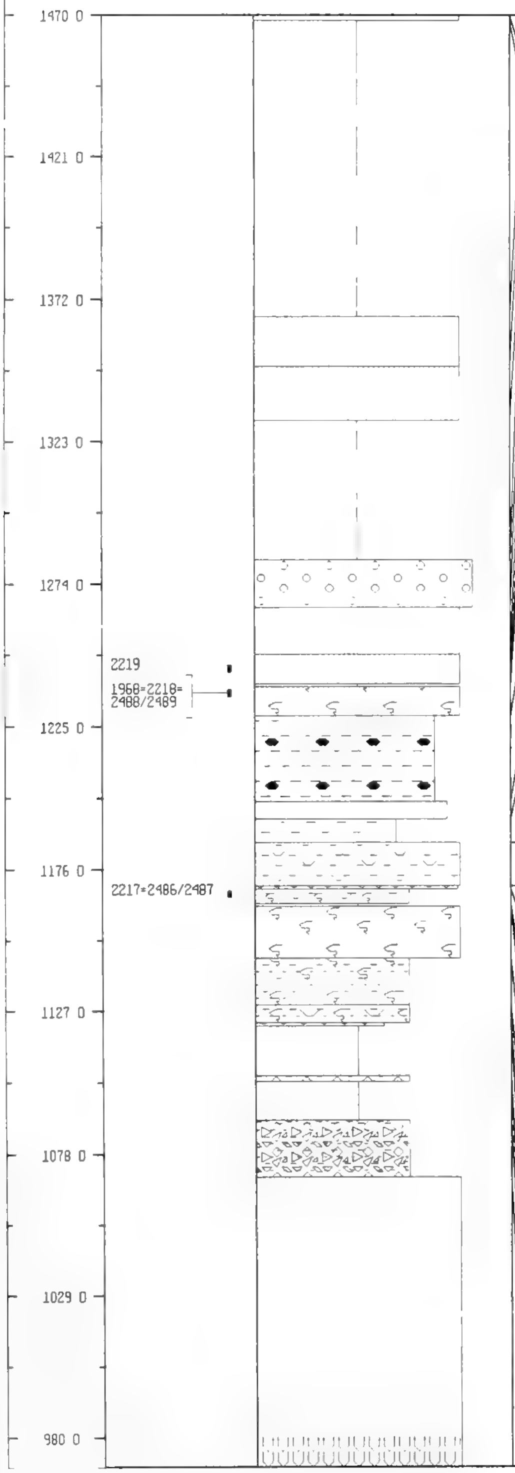
NO EXPOSURE 5 5m

SANDSTONE Coarse, gritty, calcified, shelly, volcanic

**BASE OF TOBABE SANDSTONE**

BOCAS DEL TORO BASIN Section 15

Valiente Peninsula, Southern Coast



TOP OF UNNAMED UNIT

SANDSTONE Grey, coarse, arkosic, with wood fragments 2-3cm in diameter

NO EXPOSURE 100m

SANDSTONE Weathered, ashy, coarse, volcanic, with scattered pebbles 2-3 cm thick and conglomerate beds with rounded pebbles

SANDSTONE Blue-grey, variegated, weathered, tuffaceous, greasy Includes thin-bedded, coarse sandstone with 1-m-thick, high-angle foresets of pebbly conglomerate

NO EXPOSURE 47m

PEBBLY SANDSTONE Polymict, poorly sorted, with subangular, point-bar-like cross beds, rip-up clasts of mudstone, bivalves, molds, leaves, common wood

SANDSTONE Volcanic, conglomeratic, streaky bedded with basalt cobbles Pebbles flat sided, rounded edges, polymict alternating with swaly lensing sandstone with scattered pebbles

SANDSTONE Thick, even bedded, medium grained, arkosic and slightly shaly, with mollusks and large benthic foraminifera

NO EXPOSURE 1m

SANDSTONE Muddy, silty, volcanic Unsorted, massive, lignitic (50' high bluffs), with abundant clasts to pebble size, occasional cobbles, dense shell beds, diverse snails, clams, cupuladrian and other bryozoans, pervasive bioturbation

SILTSTONE & SANDSTONE Massive, thick bedded, blue grey, muddy, occasional laminated with regular even bedding, concretion horizons 5-10 cm thick

F SANDSTONE Silty, gritty, pebbly, volcanic

MUDSTONE Tuffaceous, very regular laminated sequence Bentonites?

SILTY SANDSTONE Volcanic, with sparse scattered mollusks

CONGLOMERATE Coarse, volcanic

SILTSTONE Muddy, burrow mottled, with abundant, moderately diverse clams/snails

NO EXPOSURE 0 5m

SANDSTONE Blue-grey, burrow mottled, medium-coarse, evenly and regularly bedded, volcanic Small-scale, low, cross beds

CLAYEY SILTSTONE Blue-grey, burrow mottled, laminated, greasy, bentonitic tuffaceous

CLAYEY SILTSTONE Blue-grey, massive, with pervasive bioturbation, scattered large mollusks (cones)

CONGLOMERATIC SILTSTONE Cobbly, pebbly, shell bed rich in vermetids or Serpulorbis

NO EXPOSURE 16m

CLAYEY SILTSTONE With tuffaceous sandstone and breccia

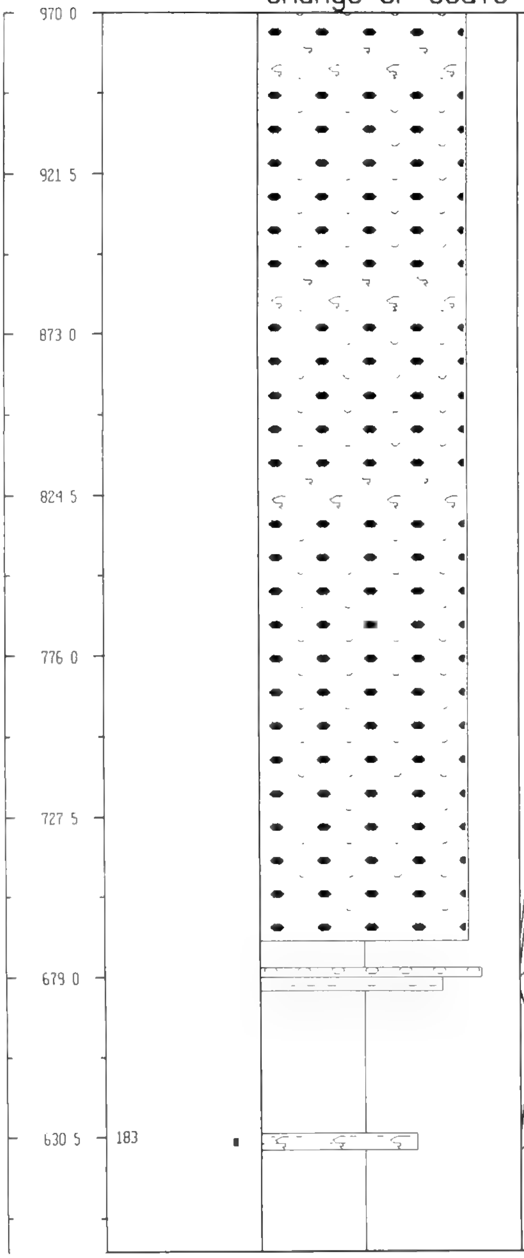
NO EXPOSURE 15m

CLAYEY SILTSTONE Blue-grey, alternating tuffaceous sandstone and thin breccia Abundant plant fragments

SANDSTONE Blue-grey, tuffaceous, laminated Alternating cobble conglomerates 10-20cm thick Sandstone has low cross beds, shallow channelling, rip-up clasts and pull aparts Minor interbedded purple-grey mudstone

Change of Scale

Section 15, contd.



SANDSTONE Massive, evenly bedded, tuffaceous, with irregular concretions, scattered mollusks and volcanic pebbles, pervasive bioturbation, ripple beds Occasional neitheids, Pecten

BASE OF UNNAMED UNIT

TOP OF SHARKHOLE POINT FORMATION

NO EXPOSURE 8m

CONGLOMERATIC SANDSTONE Evenly laminated, medium-thick bedded, arkosic, fine pebbly conglomerate and minor siltstone

SANDSTONE & SILTSTONE Coarse, quartoze, volcanic Occasional mollusk molds

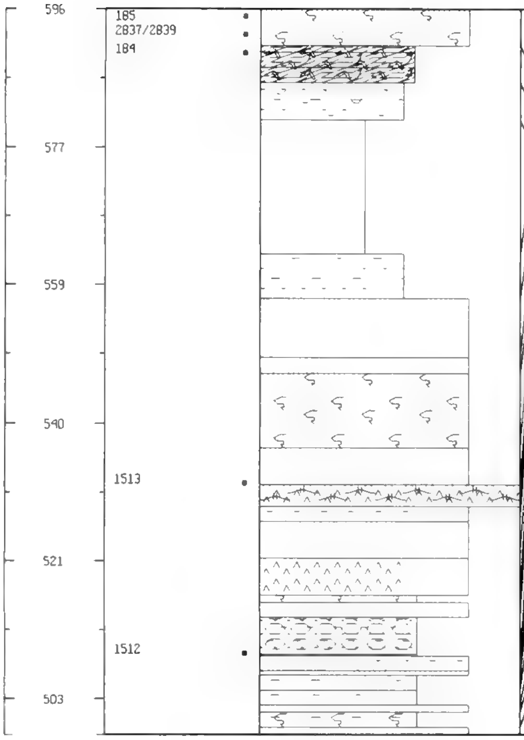
NO EXPOSURE 42m

CLAYEY SILTSTONE Medium bedded, siliceous, greasy, bentonitic? Occasional tuffaceous sandstone, thin breccias, plant debris, white-tan tuffaceous appearance, burrow mottled

NO EXPOSURE 30m

Change of Scale

Section 15, contd



SANDSTONE Greywacke, blue-grey, lignitic, muddy, quartoze, micaceous Pervasive bioturbation

**(PATTERSON CAY)**

CROSS BEDDED SILTSTONE Micaceous, blue, lignitic Pervasive bioturbation Sandstone rolls, rip-up clasts

CLAYSTONE & SILTSTONE Massive, silty and clayey, with scattered, sparse mollusks *Oliva* common, scaphopods

NO EXPOSURE 18m

**BASE SHARKHOLE POINT FORMATION**

CLAYSTONE & SILTSTONE Convoluted, laminated

**TOP NANCY POINT FORMATION**

SANDSTONE Massive, coarse, volcanic, packed with laminated and elongate, convoluted siltstone and clayey siltstone clasts 1-25 cm long

SANDSTONE With rip-up horizons, of rounded and rolled clasts, 5-15cm-diameter

SANDSTONE Massive, bioturbated, volcanic

SANDSTONE Coarse, volcanic Highly convoluted beds and rip-up clasts

ASH BEDS Bentonites

SILTY SANDSTONE Volcanic

SANDSTONE Pale, grey, ashy

SANDSTONE Fine, white, ashy, volcanic Bentonites 2-5 cm thick

SILTSTONE Intensely burrowed, laminated

SANDSTONE Coarse, volcanic, clast supported Debris flow?

CLAYEY SILTSTONE Fine conglomerate boulders, volcanic with rip-up clasts Debris flows or extremely mobile soft sediment deformation

CONGLOMERATIC SILTSTONE Fine pebbly, with lath-like clasts 2-4" long and channels 1m in relief

SILTY SANDSTONE Convolute, laminated clasts in volcanic matrix

SANDSTONE Coarse

SILTSTONE Fine, laminated, with soft sediment convolute bedding

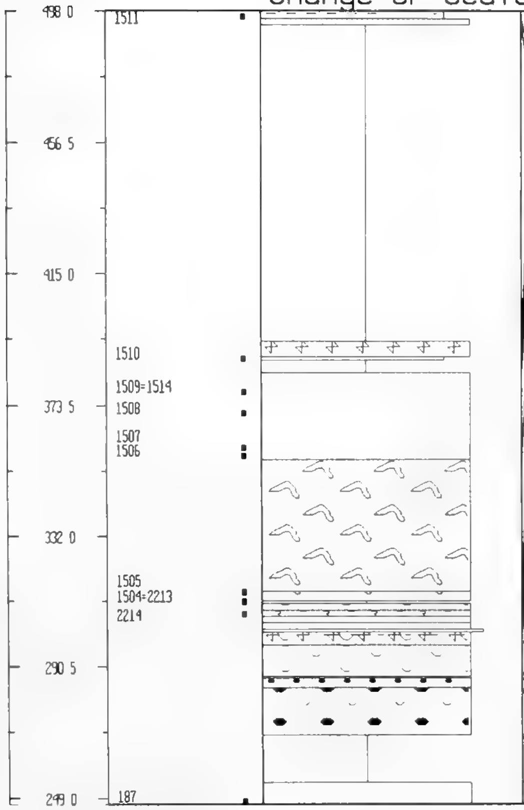
SILTSTONE Massive, coarse, tuffaceous, gritty Abundant subangular and rounded clasts 5-10cm, small, lath-like Grain supported, debris flow?

SANDSTONE Fine, with abundant rip-up clasts

SILTSTONE Laminated, with burrows with concave minisci

SANDSTONE Coarse, volcanic

Change of Scale



SANDSTONE & SILTSTONE Fine, volcanic, tuffaceous, with abundant laminated siltstone rip-ups, rounded siltstone boulders, 10-cm thick rip ups, 20-30cm long, lense-like, swirled

SANDSTONE Massive, coarse, volcanic, with alternating crystalline, tuffaceous siltstone

NO EXPOSURE 100m

SANDSTONE Massive, with siltstone rip-up clasts, rounded and angular, and small wood fragments

SANDSTONE & SILTSTONE Coarse, blue-grey, with wood fragments, benthic foraminifera

NO EXPOSURE 4m

SANDSTONE Massive, coarse, volcanic, with occasional silty and clayey strong channels and rip up clasts, pockets of conglomerate

SANDSTONE Coarse, volcanic with increasing clay matrix upward *Rhizophora* crab burrows, occasional pebbles, cross beds

SANDSTONE Massive, tan-weathering, coarse, volcanic, with occasional lenses of *Pecten* and *Chlamys*, discrete burrows, arthropod galleries

NO EXPOSURE 1m

SANDSTONE Coarse gritty, volcanic, with shell bed with small pectinoids, oysters, thick-shelled oyster, *Isognomon*

SANDSTONE Coarse, gritty, volcanic, with occasional cobbles, scattered mollusks, 2-5-cm circular burrows weathering out

SILTY SANDSTONE Regularly bedded

SANDSTONE Coarse, volcanic, with scattered snails, clams, shell hash, large arthropod burrows

PEBBLY SANDSTONE Coarse

SILTY SANDSTONE Massive, pervasively burrowed, tan weathering Cobbles, small logs and wood fragments Scattered, even shell hash Whole, disarticulated shells

SANDSTONE Shelly or hashy, coarse, with biotite, plagioclase and quartz

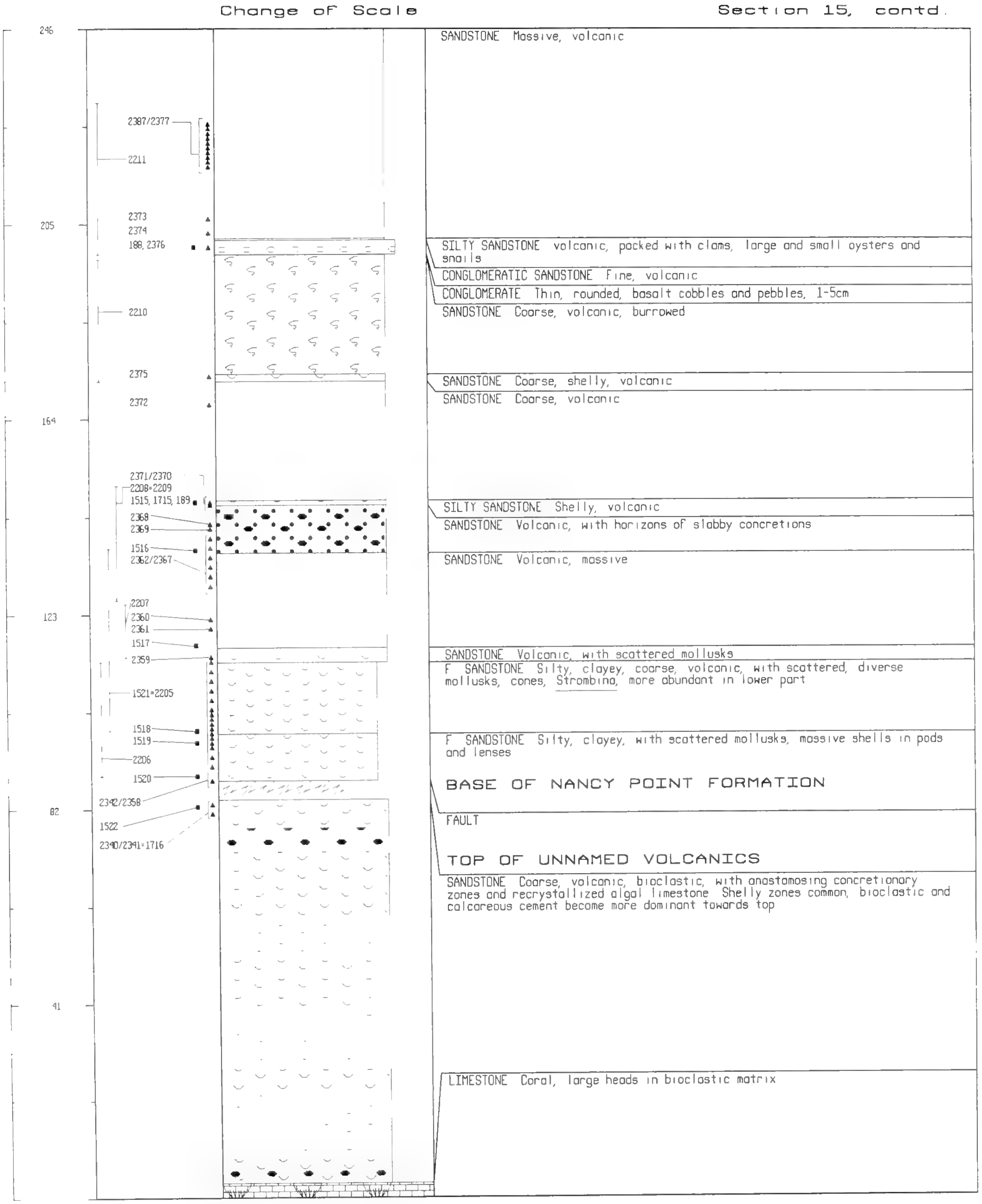
SILTY SANDSTONE Fine, with coarse, *Dosinia*-like, thick-shelled log deposit 4-5cm thick

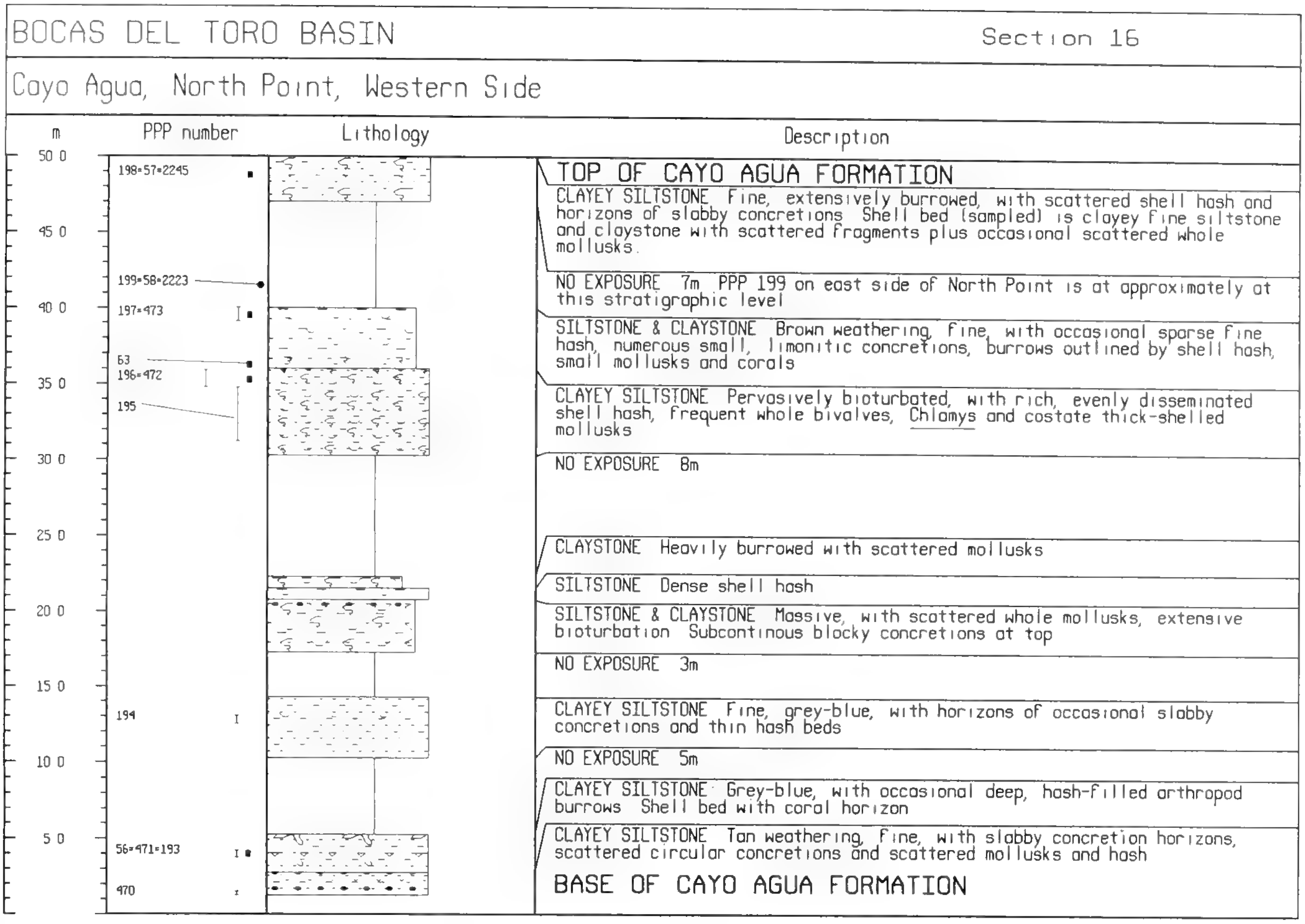
SILTY SANDSTONE With horizon of large lense-like or slabby concretions

SANDSTONE Coarse, volcanic, poorly sorted, highly feldspathic, with scattered, leached shells and small, 5-8 cm concretions

NO EXPOSURE 15m

SANDSTONE Blue-grey, volcanic, massive, gritty, poorly sorted feldspathic


Change of Scale
Section 15, contd.
246
205
164
123
82
41
2387/2377
2211
2373
2374
188, 2376
2210
2375
2372
2371/2370
2208=2209
1515, 1715, 189
2368
2369
1516
2362/2367
2207
2360
2361
1517
2359
1521=2205
1518
1519
2206
1520
2342/2358
1522
2340/2341=1716
SANDSTONE Massive, volcanic
SILTY SANDSTONE volcanic, packed with clams, large and small oysters and snails
CONGLOMERATIC SANDSTONE Fine, volcanic
CONGLOMERATE Thin, rounded, basalt cobbles and pebbles, 1-5cm
SANDSTONE Coarse, volcanic, burrowed
SANDSTONE Coarse, shelly, volcanic
SANDSTONE Coarse, volcanic
SILTY SANDSTONE Shelly, volcanic
SANDSTONE Volcanic, with horizons of slabby concretions
SANDSTONE Volcanic, massive
SANDSTONE Volcanic, with scattered mollusks
F SANDSTONE Silty, clayey, coarse, volcanic, with scattered, diverse mollusks, cones, Strombina, more abundant in lower part
F SANDSTONE Silty, clayey, with scattered mollusks, massive shells in pods and lenses
BASE OF NANCY POINT FORMATION
FAULT
TOP OF UNNAMED VOLCANICS
SANDSTONE Coarse, volcanic, bioclastic, with anastomosing concretionary zones and recrystallized algal limestone Shelly zones common, bioclastic and calcareous cement become more dominant towards top
LIMESTONE Coral, large heads in bioclastic matrix



BOCAS DEL TORO BASIN — Section 16

Cayo Agua, North Point, Western Side

TOP OF CAYO AGUA FORMATION

CLAYEY SILTSTONE Fine, extensively burrowed, with scattered shell hash and horizons of slabby concretions Shell bed (sampled) is clayey fine siltstone and claystone with scattered fragments plus occasional scattered whole mollusks.

NO EXPOSURE 7m PPP 199 on east side of North Point is at approximately at this stratigraphic level

SILTSTONE & CLAYSTONE Brown weathering, fine, with occasional sparse fine hash, numerous small, limonitic concretions, burrows outlined by shell hash, small mollusks and corals

CLAYEY SILTSTONE Pervasively bioturbated, with rich, evenly disseminated shell hash, frequent whole bivalves, Chlamys and costate thick-shelled mollusks

NO EXPOSURE 8m

CLAYSTONE Heavily burrowed with scattered mollusks

SILTSTONE Dense shell hash

SILTSTONE & CLAYSTONE Massive, with scattered whole mollusks, extensive bioturbation Subcontinous blocky concretions at top

NO EXPOSURE 3m

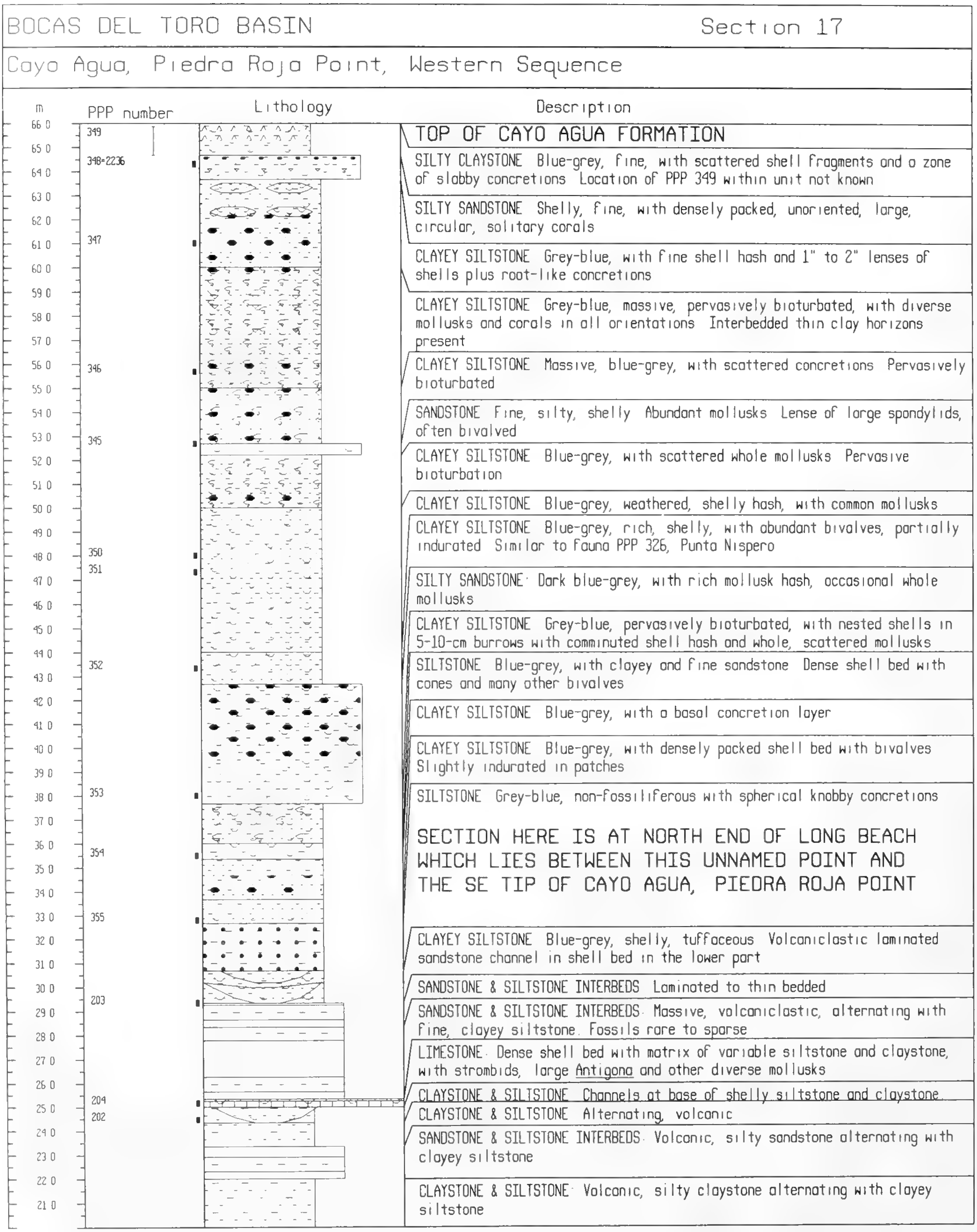
CLAYEY SILTSTONE Fine, grey-blue, with horizons of occasional slabby concretions and thin hash beds

NO EXPOSURE 5m

CLAYEY SILTSTONE Grey-blue, with occasional deep, hash-filled arthropod burrows Shell bed with coral horizon

CLAYEY SILTSTONE Tan weathering, fine, with slabby concretion horizons, scattered circular concretions and scattered mollusks and hash

BASE OF CAYO AGUA FORMATION



TOP OF CAYO AGUA FORMATION

SILTY CLAYSTONE Blue-grey, fine, with scattered shell fragments and a zone of slabby concretions Location of PPP 349 within unit not known

SILTY SANDSTONE Shelly, fine, with densely packed, unoriented, large, circular, solitary corals

CLAYEY SILTSTONE Grey-blue, with fine shell hash and 1" to 2" lenses of shells plus root-like concretions

CLAYEY SILTSTONE Grey-blue, massive, pervasively bioturbated, with diverse mollusks and corals in all orientations Interbedded thin clay horizons present

CLAYEY SILTSTONE Massive, blue-grey, with scattered concretions Pervasively bioturbated

SANDSTONE Fine, silty, shelly Abundant mollusks Lense of large spondylids, often bivalved

CLAYEY SILTSTONE Blue-grey, with scattered whole mollusks Pervasive bioturbation

CLAYEY SILTSTONE Blue-grey, weathered, shelly hash, with common mollusks

CLAYEY SILTSTONE Blue-grey, rich, shelly, with abundant bivalves, partially indurated Similar to fauna PPP 326, Punta Nispero

SILTY SANDSTONE· Dark blue-grey, with rich mollusk hash, occasional whole mollusks

CLAYEY SILTSTONE Grey-blue, pervasively bioturbated, with nested shells in 5-10-cm burrows with comminuted shell hash and whole, scattered mollusks

SILTSTONE Blue-grey, with clayey and fine sandstone Dense shell bed with cones and many other bivalves

CLAYEY SILTSTONE Blue-grey, with a basal concretion layer

CLAYEY SILTSTONE Blue-grey, with densely packed shell bed with bivalves Slightly indurated in patches

SILTSTONE Grey-blue, non-fossiliferous with spherical knobby concretions

SECTION HERE IS AT NORTH END OF LONG BEACH WHICH LIES BETWEEN THIS UNNAMED POINT AND THE SE TIP OF CAYO AGUA, PIEDRA ROJA POINT

CLAYEY SILTSTONE Blue-grey, shelly, tuffaceous Volcaniclastic laminated sandstone channel in shell bed in the lower part

SANDSTONE & SILTSTONE INTERBEDS Laminated to thin bedded

SANDSTONE & SILTSTONE INTERBEDS· Massive, volcaniclastic, alternating with fine, clayey siltstone. Fossils rare to sparse

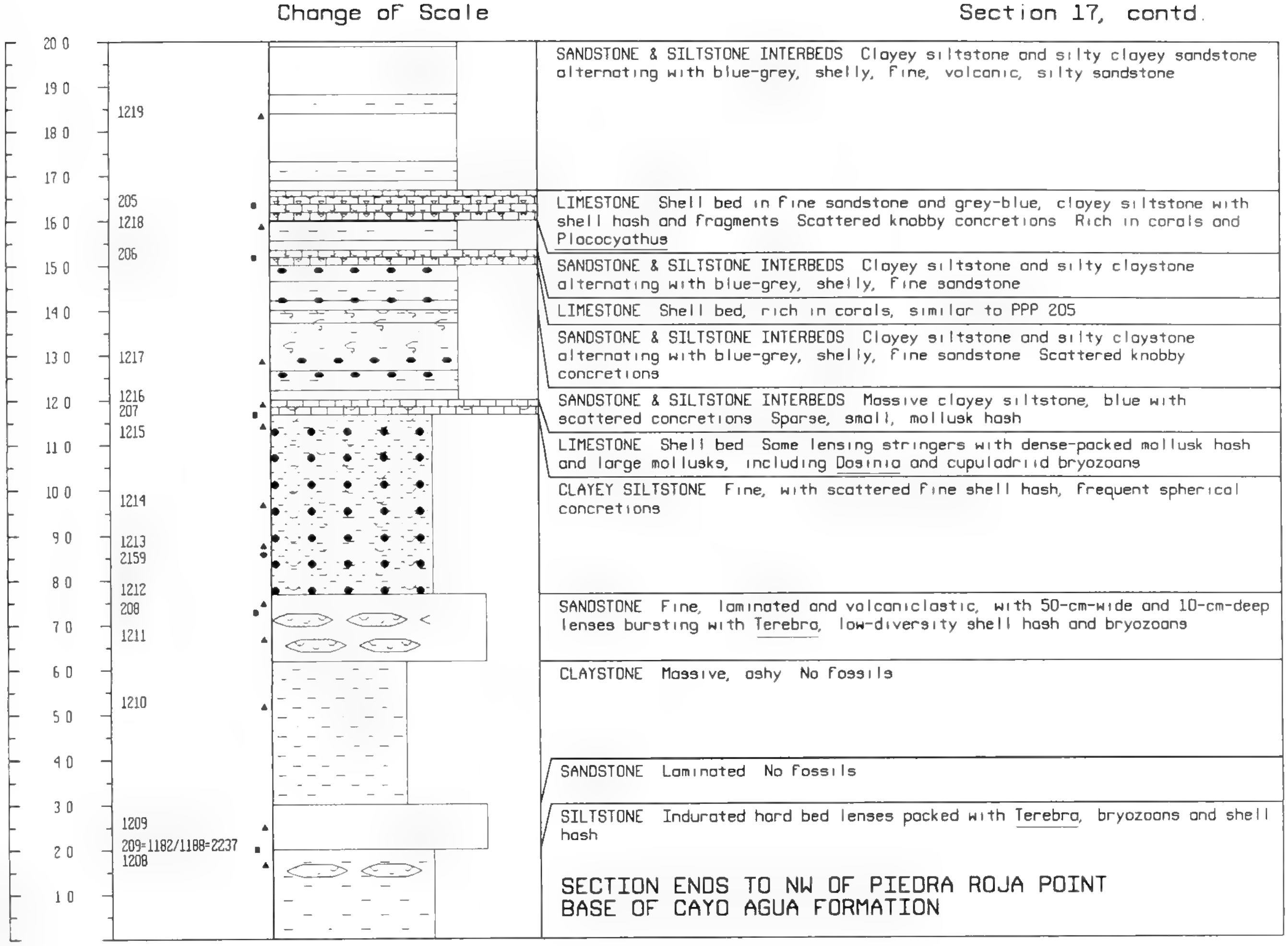
LIMESTONE· Dense shell bed with matrix of variable siltstone and claystone, with strombids, large *Antigona* and other diverse mollusks

CLAYSTONE & SILTSTONE Channels at base of shelly siltstone and claystone

CLAYSTONE & SILTSTONE Alternating, volcanic

SANDSTONE & SILTSTONE INTERBEDS· Volcanic, silty sandstone alternating with clayey siltstone

CLAYSTONE & SILTSTONE· Volcanic, silty claystone alternating with clayey siltstone



SANDSTONE & SILTSTONE INTERBEDS Clayey siltstone and silty clayey sandstone alternating with blue-grey, shelly, fine, volcanic, silty sandstone

LIMESTONE Shell bed in fine sandstone and grey-blue, clayey siltstone with shell hash and fragments Scattered knobby concretions Rich in corals and Placocyathus

SANDSTONE & SILTSTONE INTERBEDS Clayey siltstone and silty claystone alternating with blue-grey, shelly, fine sandstone

LIMESTONE Shell bed, rich in corals, similar to PPP 205

SANDSTONE & SILTSTONE INTERBEDS Clayey siltstone and silty claystone alternating with blue-grey, shelly, fine sandstone Scattered knobby concretions

SANDSTONE & SILTSTONE INTERBEDS Massive clayey siltstone, blue with scattered concretions Sparse, small, mollusk hash

LIMESTONE Shell bed Some lensing stringers with dense-packed mollusk hash and large mollusks, including Dosinia and cupuladriid bryozoans

CLAYEY SILTSTONE Fine, with scattered fine shell hash, frequent spherical concretions

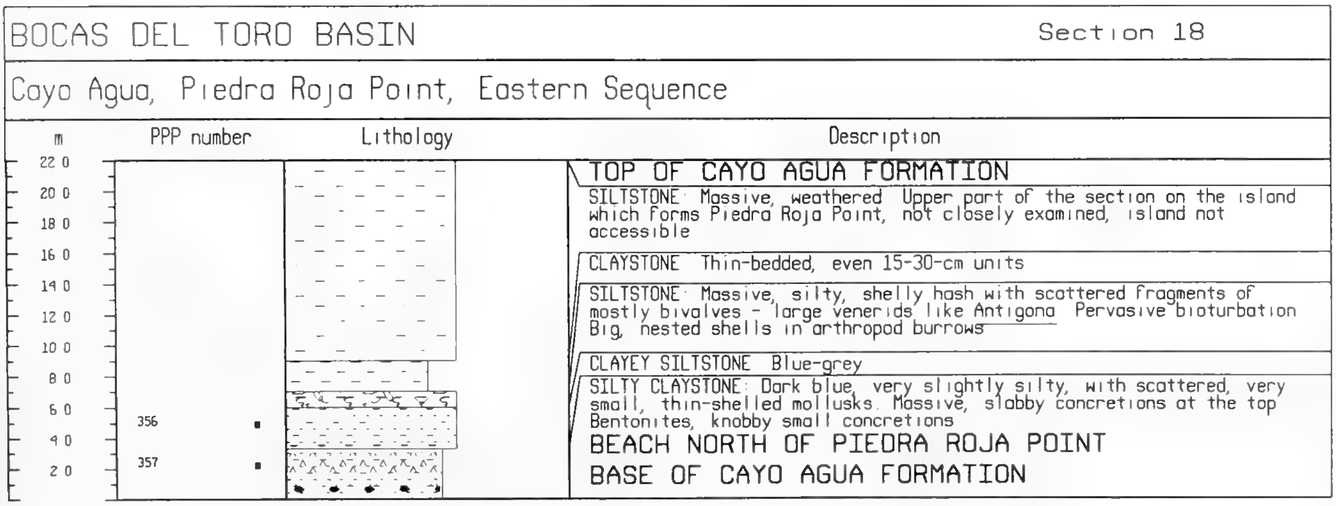
SANDSTONE Fine, laminated and volcaniclastic, with 50-cm-wide and 10-cm-deep lenses bursting with Terebra, low-diversity shell hash and bryozoans

CLAYSTONE Massive, ashy No fossils

SANDSTONE Laminated No fossils

SILTSTONE Indurated hard bed lenses packed with Terebra, bryozoans and shell hash

SECTION ENDS TO NW OF PIEDRA ROJA POINT
BASE OF CAYO AGUA FORMATION



BOCAS DEL TORO BASIN Section 18

Cayo Agua, Piedra Roja Point, Eastern Sequence

Description

TOP OF CAYO AGUA FORMATION

SILTSTONE Massive, weathered Upper part of the section on the island which forms Piedra Roja Point, not closely examined, island not accessible

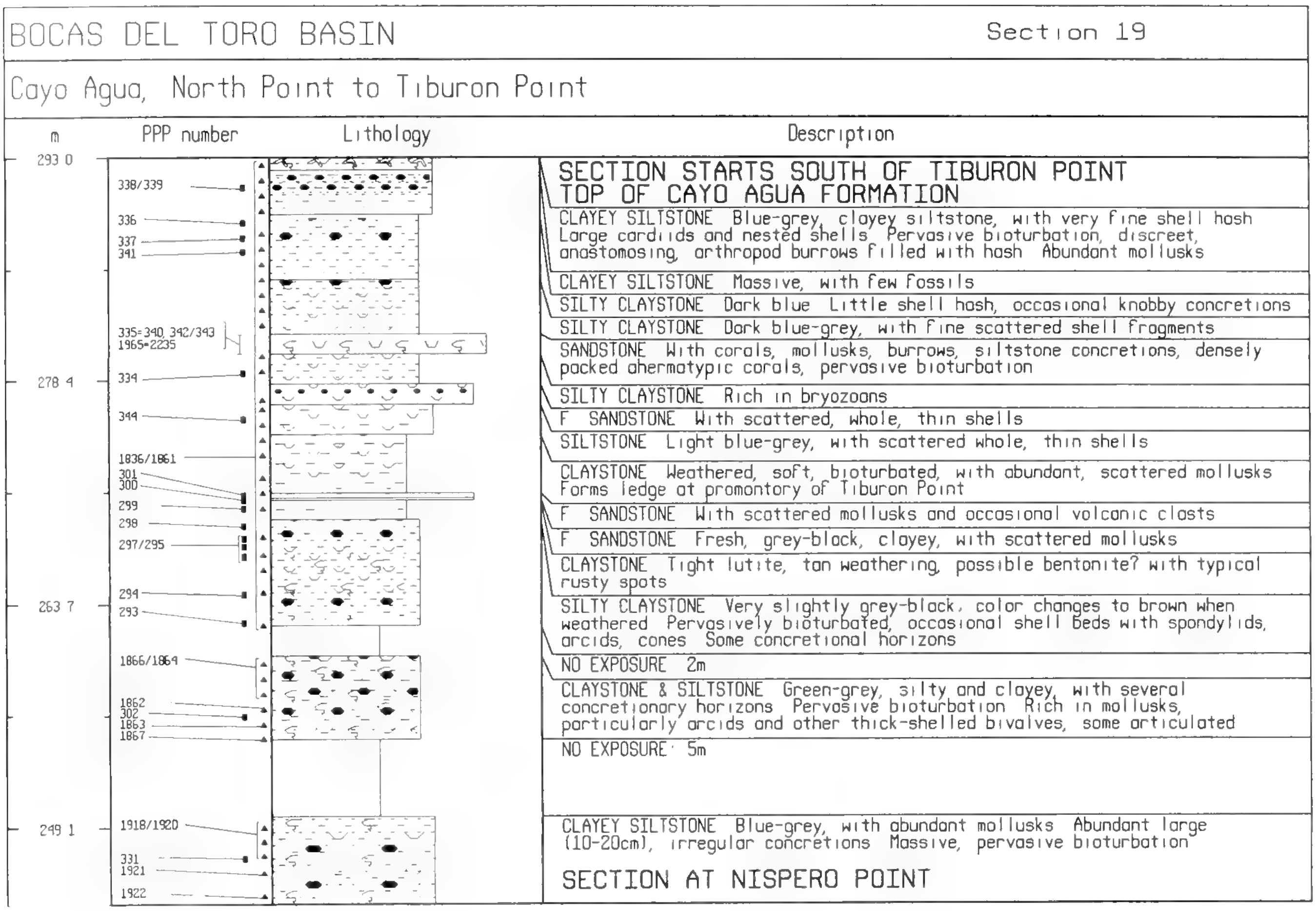
CLAYSTONE Thin-bedded, even 15-30-cm units

SILTSTONE Massive, silty, shelly hash with scattered fragments of mostly bivalves - large venerids like Antigona Pervasive bioturbation Big, nested shells in arthropod burrows

CLAYEY SILTSTONE Blue-grey

SILTY CLAYSTONE Dark blue, very slightly silty, with scattered, very small, thin-shelled mollusks Massive, slabby concretions at the top Bentonites, knobby small concretions

BEACH NORTH OF PIEDRA ROJA POINT
BASE OF CAYO AGUA FORMATION



SECTION STARTS SOUTH OF TIBURON POINT
TOP OF CAYO AGUA FORMATION

CLAYEY SILTSTONE Blue-grey, clayey siltstone, with very fine shell hash Large cardiids and nested shells Pervasive bioturbation, discreet, anastomosing, arthropod burrows filled with hash Abundant mollusks

CLAYEY SILTSTONE Massive, with few fossils

SILTY CLAYSTONE Dark blue Little shell hash, occasional knobby concretions

SILTY CLAYSTONE Dark blue-grey, with fine scattered shell fragments

SANDSTONE With corals, mollusks, burrows, siltstone concretions, densely packed ahermatypic corals, pervasive bioturbation

SILTY CLAYSTONE Rich in bryozoans

F SANDSTONE With scattered, whole, thin shells

SILTSTONE Light blue-grey, with scattered whole, thin shells

CLAYSTONE Weathered, soft, bioturbated, with abundant, scattered mollusks Forms ledge at promontory of Tiburon Point

F SANDSTONE With scattered mollusks and occasional volcanic clasts

F SANDSTONE Fresh, grey-black, clayey, with scattered mollusks

CLAYSTONE Tight lutite, tan weathering, possible bentonite? with typical rusty spots

SILTY CLAYSTONE Very slightly grey-black, color changes to brown when weathered Pervasively bioturbated, occasional shell beds with spondylids, arcids, cones Some concretional horizons

NO EXPOSURE 2m

CLAYSTONE & SILTSTONE Green-grey, silty and clayey, with several concretionary horizons Pervasive bioturbation Rich in mollusks, particularly arcids and other thick-shelled bivalves, some articulated

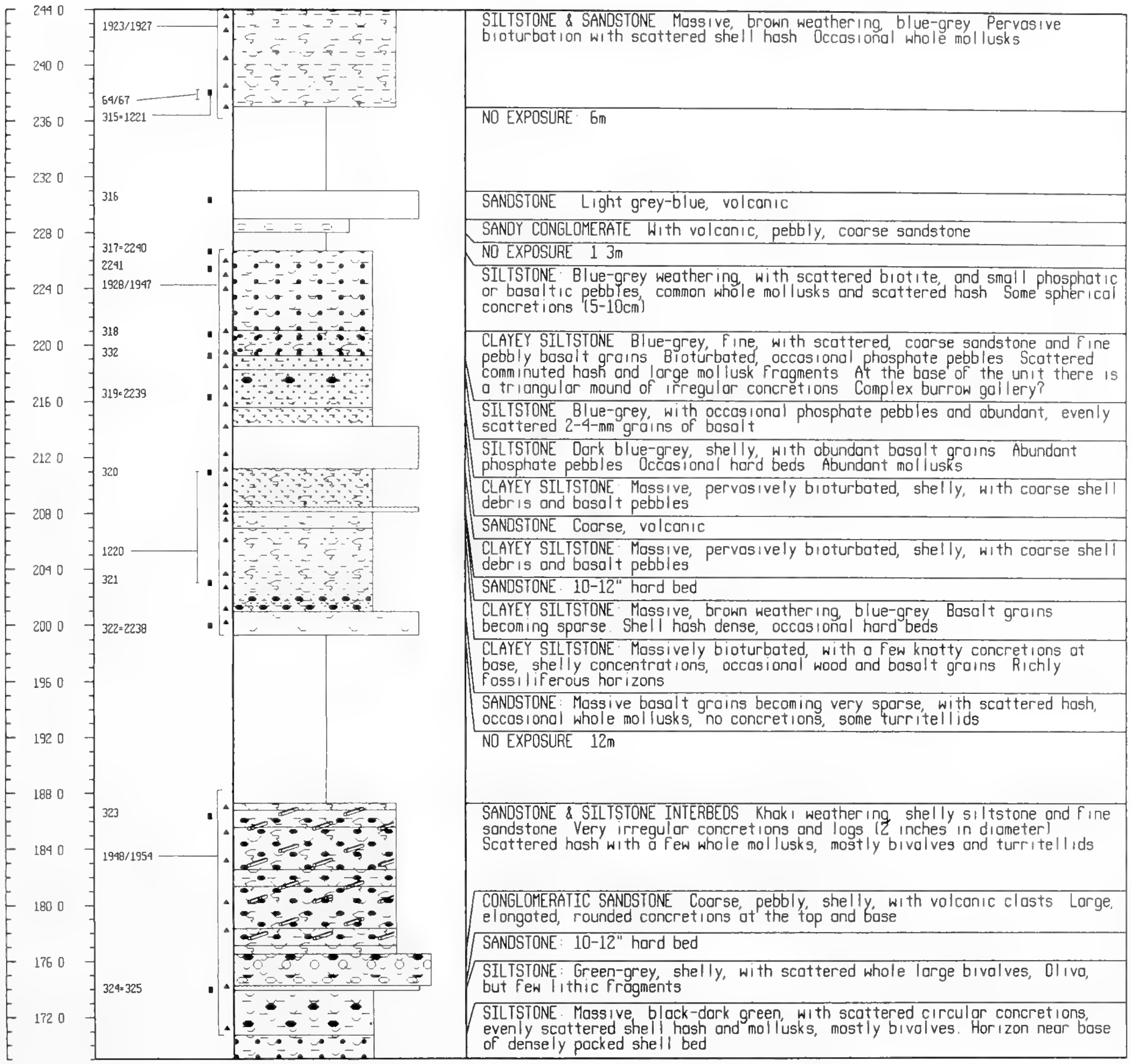
NO EXPOSURE 5m

CLAYEY SILTSTONE Blue-grey, with abundant mollusks Abundant large (10-20cm), irregular concretions Massive, pervasive bioturbation

SECTION AT NISPERO POINT

Change of Scale

Section 19, contd



SILTSTONE & SANDSTONE Massive, brown weathering, blue-grey Pervasive bioturbation with scattered shell hash Occasional whole mollusks

NO EXPOSURE 6m

SANDSTONE Light grey-blue, volcanic

SANDY CONGLOMERATE With volcanic, pebbly, coarse sandstone

NO EXPOSURE 1 3m

SILTSTONE Blue-grey weathering, with scattered biotite, and small phosphatic or basaltic pebbles, common whole mollusks and scattered hash Some spherical concretions (5-10cm)

CLAYEY SILTSTONE Blue-grey, fine, with scattered, coarse sandstone and fine pebbly basalt grains Bioturbated, occasional phosphate pebbles Scattered comminuted hash and large mollusk fragments At the base of the unit there is a triangular mound of irregular concretions Complex burrow gallery?

SILTSTONE Blue-grey, with occasional phosphate pebbles and abundant, evenly scattered 2-4-mm grains of basalt

SILTSTONE Dark blue-grey, shelly, with abundant basalt grains Abundant phosphate pebbles Occasional hard beds Abundant mollusks

CLAYEY SILTSTONE Massive, pervasively bioturbated, shelly, with coarse shell debris and basalt pebbles

SANDSTONE Coarse, volcanic

CLAYEY SILTSTONE Massive, pervasively bioturbated, shelly, with coarse shell debris and basalt pebbles

SANDSTONE 10-12" hard bed

CLAYEY SILTSTONE Massive, brown weathering, blue-grey Basalt grains becoming sparse. Shell hash dense, occasional hard beds

CLAYEY SILTSTONE Massively bioturbated, with a few knotty concretions at base, shelly concentrations, occasional wood and basalt grains Richly fossiliferous horizons

SANDSTONE: Massive basalt grains becoming very sparse, with scattered hash, occasional whole mollusks, no concretions, some turritellids

NO EXPOSURE 12m

SANDSTONE & SILTSTONE INTERBEDS Khaki weathering, shelly siltstone and fine sandstone Very irregular concretions and logs (2 inches in diameter) Scattered hash with a few whole mollusks, mostly bivalves and turritellids

CONGLOMERATIC SANDSTONE Coarse, pebbly, shelly, with volcanic clasts Large, elongated, rounded concretions at the top and base

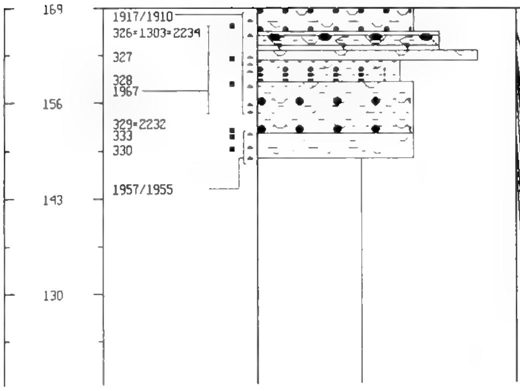
SANDSTONE: 10-12" hard bed

SILTSTONE: Green-grey, shelly, with scattered whole large bivalves, Oliva, but few lithic fragments

SILTSTONE Massive, black-dark green, with scattered circular concretions, evenly scattered shell hash and mollusks, mostly bivalves. Horizon near base of densely packed shell bed

Change of Scale

Section 19, contd.



SILTSTONE Massive, black-dark green, with scattered circular concretions, evenly scattered shell hash and mollusks, mostly bivalves Horizon near base of densely packed shell bed

SILTSTONE & SANDSTONE INTERBEDS Massive, bioturbated, silty shelly hash Few whole mollusks, common fine, basaltic clasts The siltstone is interbedded with coarse sandstone with logs and wood flakes, scattered concretions Pervasive bioturbation with occasional burrows Some turritellids

C SANDSTONE Coarse, volcanic, with elongate, root-like concretions Rich in mollusks Grades basally into siltstone Rich in mollusks

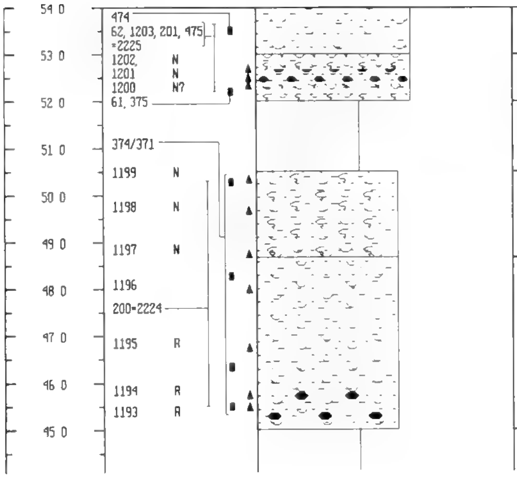
SILTY CLAYSTONE Massive, green-grey, with shell hash, scattered small knobby concretions, abundant lithic grains of basalt, (2-4 mm) Occasional bentonitic horizons

CLAYEY SILTSTONE Blue-grey, rich in fine, comminuted shell hash, with scattered lithic fragments and knobby concretions Rich in mollusks at top

SILTSTONE Blue-grey, fine shelly, with occasional large, irregular burrows, shell hash dense and abundant but finely comminuted Occasional whole bivalves, no lithic clasts Some large strombids (Melongena)

NO EXPOSURE 94 5m

Change of Scale



CLAYEY SILTSTONE With scattered fine hash

CLAYEY SILTSTONE Grey-blue, with diffuse, finely scattered shell hash, rich in diverse mollusks (vermetids, serpulids), rare corals Very bioturbated

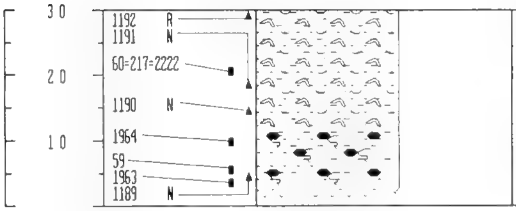
NO EXPOSURE 1 5m

SILTY CLAYSTONE Grey-black, fine, rich in scattered mollusks Massive pervasive bioturbation

SILTY CLAYSTONE With abundant shells, concretions at base

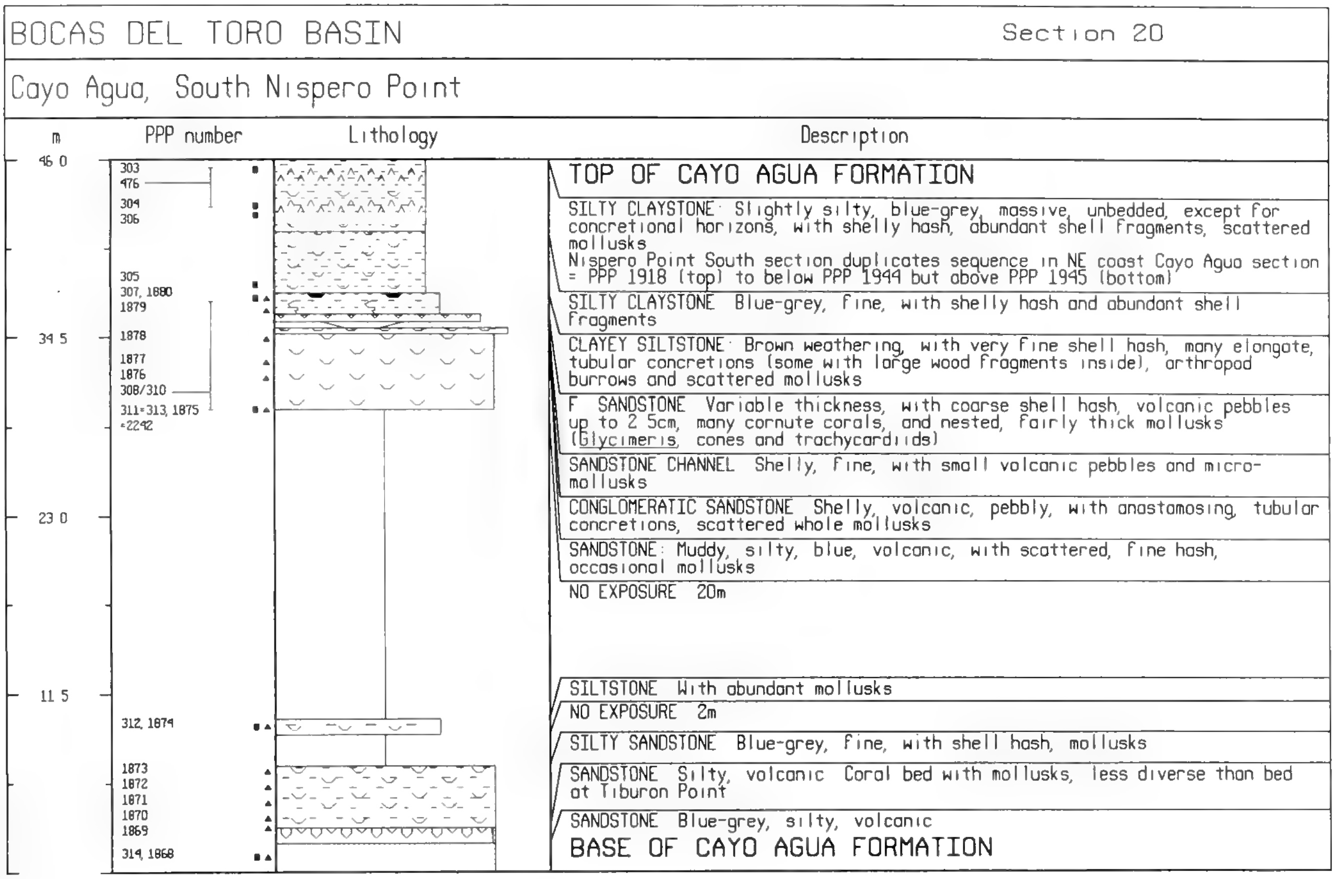
NO EXPOSURE Thickness of unexposed interval is 41 3m

Change of Scale



SILTY CLAYSTONE Very slightly, massive, unbedded, grey-black, with micromollusks, scattered hash and small arthropod burrows, bioturbation

CAYO AGUA NE COAST, SOUTH OF NORTH POINT
BASE OF CAYO AGUA FORMATION



BOCAS DEL TORO BASIN Section 20

Cayo Agua, South Nispero Point

TOP OF CAYO AGUA FORMATION

SILTY CLAYSTONE: Slightly silty, blue-grey, massive, unbedded, except for concretional horizons, with shelly hash, abundant shell fragments, scattered mollusks

Nispero Point South section duplicates sequence in NE coast Cayo Agua section = PPP 1918 (top) to below PPP 1944 but above PPP 1945 (bottom)

SILTY CLAYSTONE Blue-grey, fine, with shelly hash and abundant shell fragments

CLAYEY SILTSTONE: Brown weathering, with very fine shell hash, many elongate, tubular concretions (some with large wood fragments inside), arthropod burrows and scattered mollusks

F SANDSTONE Variable thickness, with coarse shell hash, volcanic pebbles up to 2 5cm, many cornute corals, and nested, fairly thick mollusks (Glycimeris, cones and trachycardiids)

SANDSTONE CHANNEL Shelly, fine, with small volcanic pebbles and micromollusks

CONGLOMERATIC SANDSTONE Shelly, volcanic, pebbly, with anastomosing, tubular concretions, scattered whole mollusks

SANDSTONE: Muddy, silty, blue, volcanic, with scattered, fine hash, occasional mollusks

NO EXPOSURE 20m

SILTSTONE With abundant mollusks

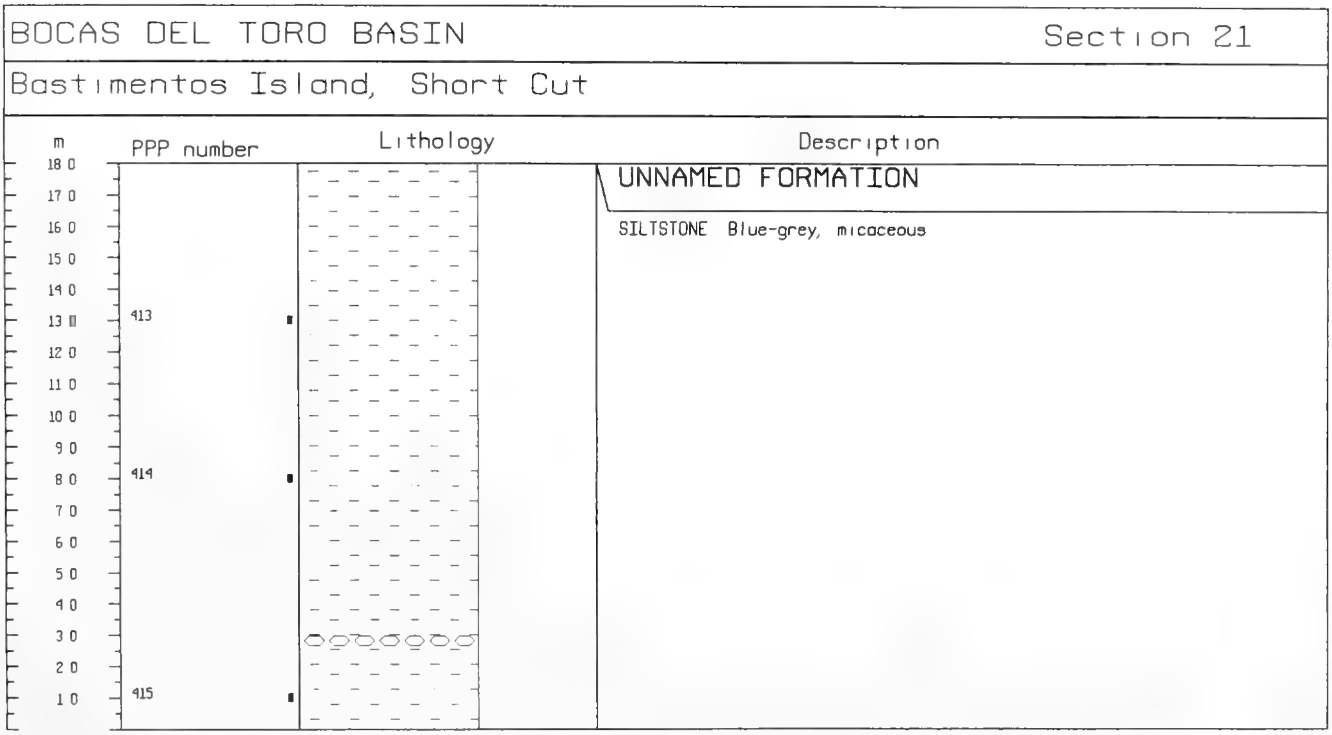
NO EXPOSURE 2m

SILTY SANDSTONE Blue-grey, fine, with shell hash, mollusks

SANDSTONE Silty, volcanic Coral bed with mollusks, less diverse than bed at Tiburon Point

SANDSTONE Blue-grey, silty, volcanic

BASE OF CAYO AGUA FORMATION

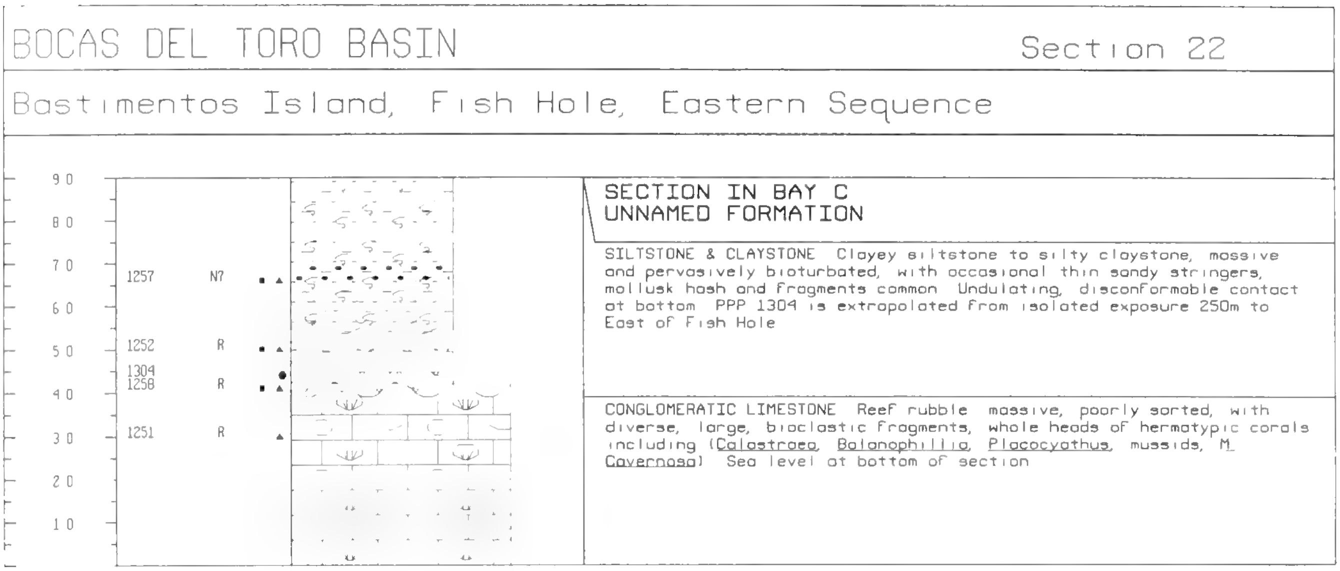


BOCAS DEL TORO BASIN Section 21

Bastimentos Island, Short Cut

UNNAMED FORMATION

SILTSTONE Blue-grey, micaceous



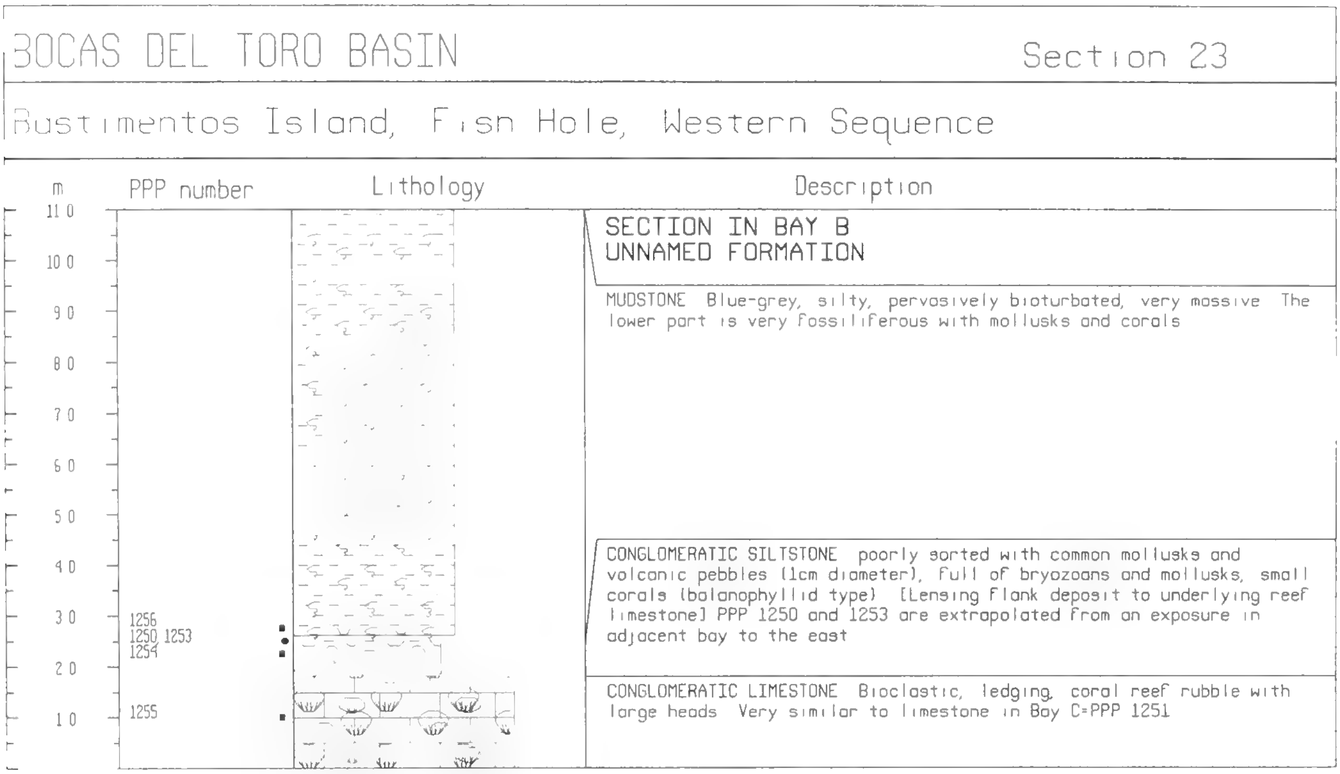
BOCAS DEL TORO BASIN Section 22

Bastimentos Island, Fish Hole, Eastern Sequence

SECTION IN BAY C
UNNAMED FORMATION

SILTSTONE & CLAYSTONE Clayey siltstone to silty claystone, massive and pervasively bioturbated, with occasional thin sandy stringers, mollusk hash and fragments common Undulating, disconformable contact at bottom PPP 1304 is extrapolated from isolated exposure 250m to East of Fish Hole

CONGLOMERATIC LIMESTONE Reef rubble massive, poorly sorted, with diverse, large, bioclastic fragments, whole heads of hermatypic corals including (Calostraea, Balanophillia, Placocyathus, mussids, M Cavernosa) Sea level at bottom of section



BOCAS DEL TORO BASIN Section 23

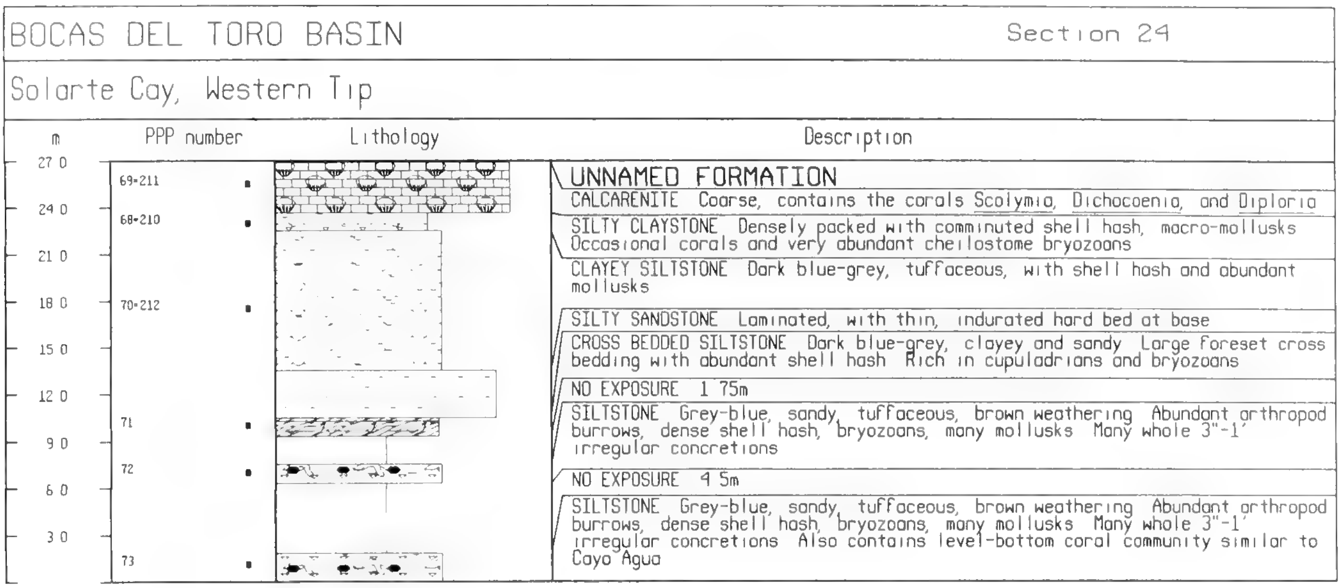
Bastimentos Island, Fish Hole, Western Sequence

SECTION IN BAY B
UNNAMED FORMATION

MUDSTONE Blue-grey, silty, pervasively bioturbated, very massive The lower part is very fossiliferous with mollusks and corals

CONGLOMERATIC SILTSTONE poorly sorted with common mollusks and volcanic pebbles (1cm diameter), full of bryozoans and mollusks, small corals (balanophyllid type) [Lensing flank deposit to underlying reef limestone] PPP 1250 and 1253 are extrapolated from an exposure in adjacent bay to the east

CONGLOMERATIC LIMESTONE Bioclastic, ledging, coral reef rubble with large heads Very similar to limestone in Bay C=PPP 1251


BOCAS DEL TORO BASIN Section 24

Solarte Cay, Western Tip

UNNAMED FORMATION

CALCARENITE Coarse, contains the corals Scolymia, Dichocoenia, and Diploria

SILTY CLAYSTONE Densely packed with comminuted shell hash, macro-mollusks Occasional corals and very abundant cheilostome bryozoans

CLAYEY SILTSTONE Dark blue-grey, tuffaceous, with shell hash and abundant mollusks

SILTY SANDSTONE Laminated, with thin, indurated hard bed at base

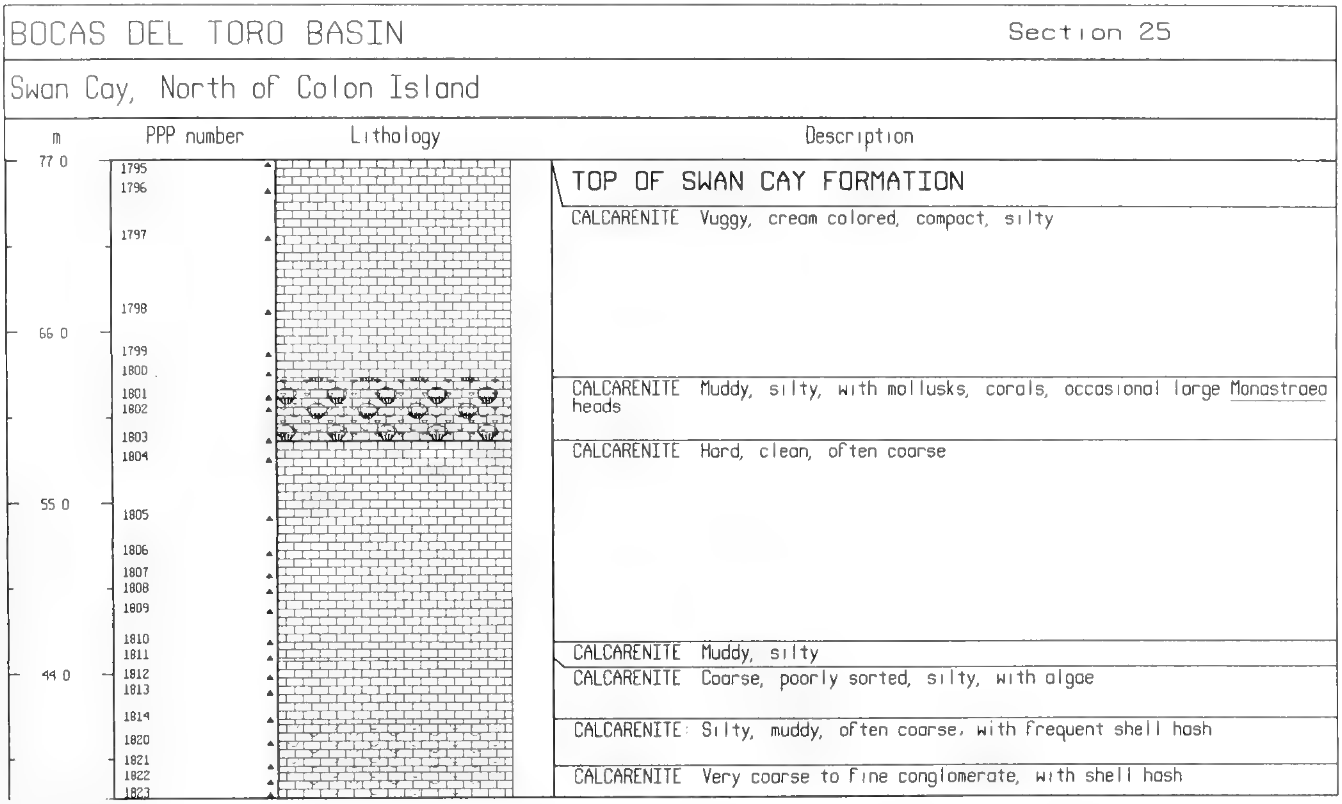
CROSS BEDDED SILTSTONE Dark blue-grey, clayey and sandy Large foreset cross bedding with abundant shell hash Rich in cupuladrians and bryozoans

NO EXPOSURE 1 75m

SILTSTONE Grey-blue, sandy, tuffaceous, brown weathering Abundant arthropod burrows, dense shell hash, bryozoans, many mollusks Many whole 3"-1' irregular concretions

NO EXPOSURE 4 5m

SILTSTONE Grey-blue, sandy, tuffaceous, brown weathering Abundant arthropod burrows, dense shell hash, bryozoans, many mollusks Many whole 3"-1' irregular concretions Also contains level-bottom coral community similar to Cayo Agua


BOCAS DEL TORO BASIN Section 25

Swan Cay, North of Colon Island

TOP OF SWAN CAY FORMATION

CALCARENITE Vuggy, cream colored, compact, silty

CALCARENITE Muddy, silty, with mollusks, corals, occasional large Monastraea heads

CALCARENITE Hard, clean, often coarse

CALCARENITE Muddy, silty

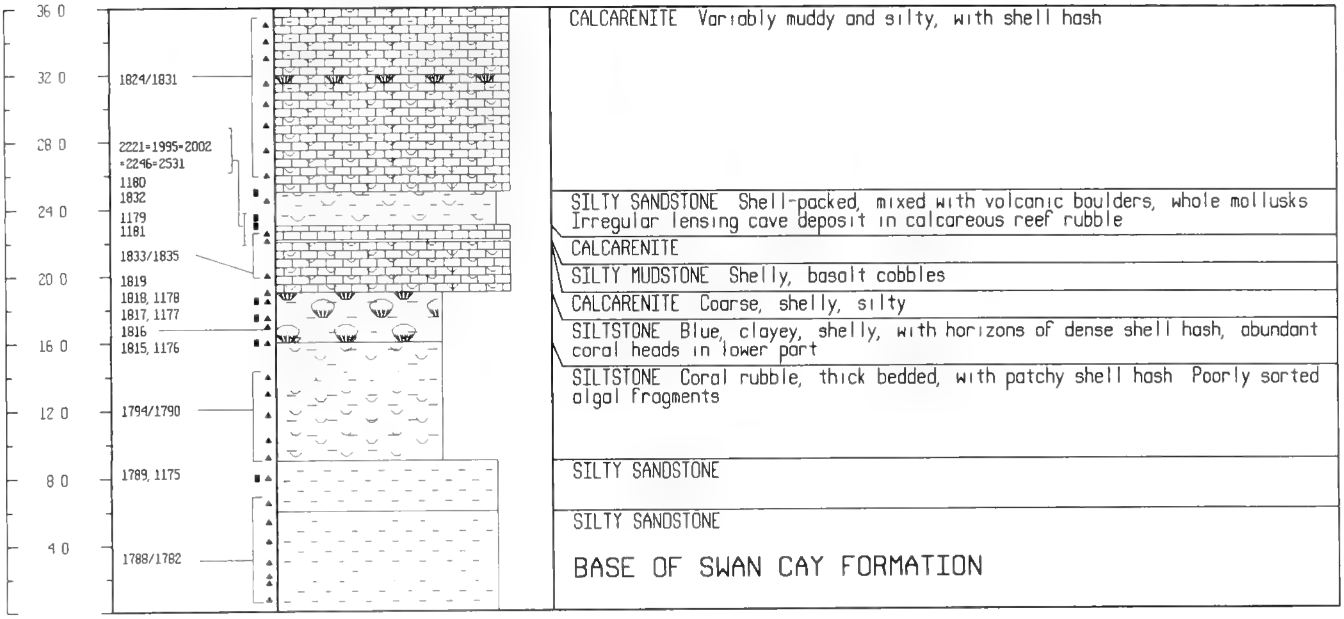
CALCARENITE Coarse, poorly sorted, silty, with algae

CALCARENITE Silty, muddy, often coarse, with frequent shell hash

CALCARENITE Very coarse to fine conglomerate, with shell hash

Change of Scale

Section 25, contd



CALCARENITE Variably muddy and silty, with shell hash

SILTY SANDSTONE Shell-packed, mixed with volcanic boulders, whole mollusks Irregular lensing cave deposit in calcareous reef rubble

CALCARENITE

SILTY MUDSTONE Shelly, basalt cobbles

CALCARENITE Coarse, shelly, silty

SILTSTONE Blue, clayey, shelly, with horizons of dense shell hash, abundant coral heads in lower part

SILTSTONE Coral rubble, thick bedded, with patchy shell hash Poorly sorted algal fragments

SILTY SANDSTONE

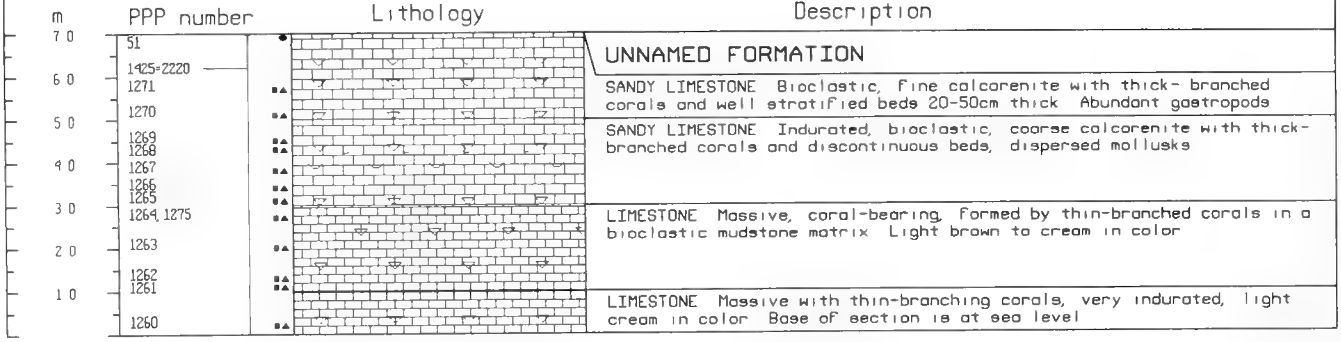
SILTY SANDSTONE

BASE OF SWAN CAY FORMATION

BOCAS DEL TORO BASIN

Section 26

Colon Island, Hill Point



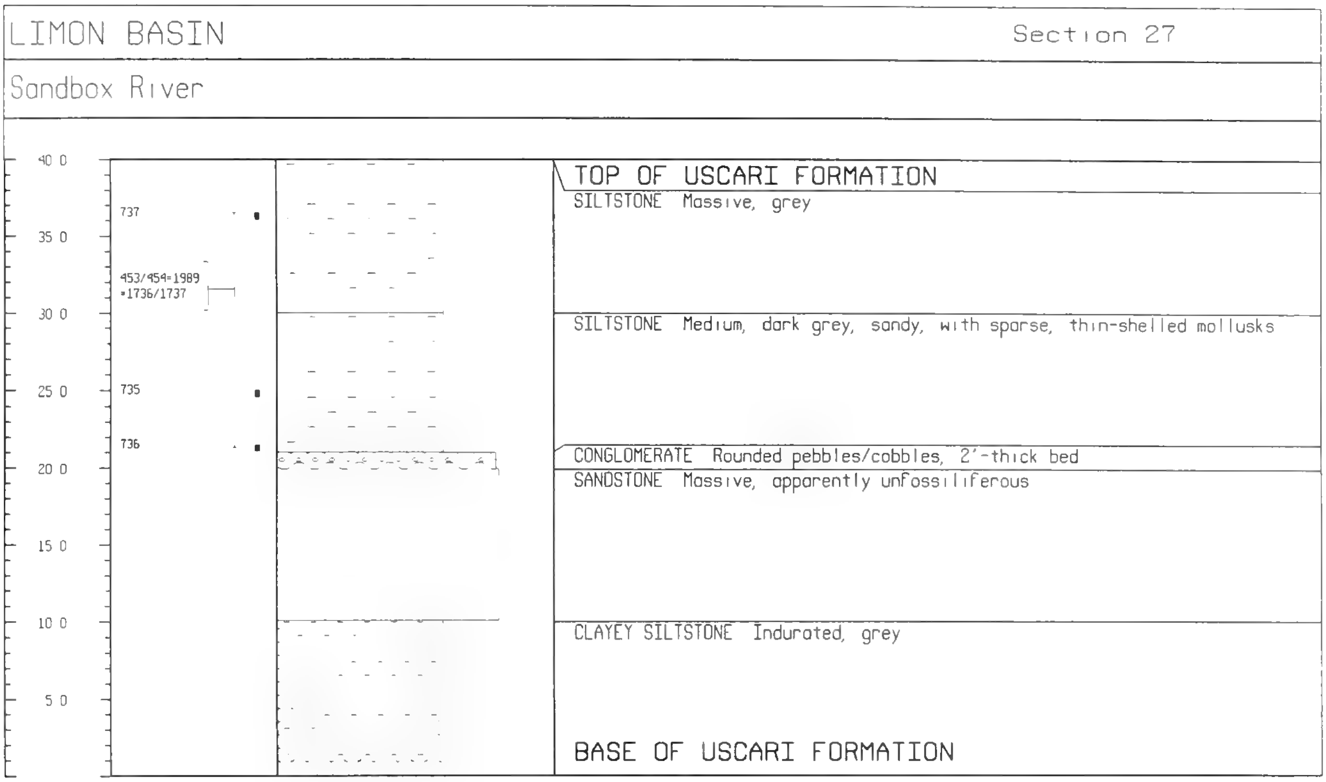
UNNAMED FORMATION

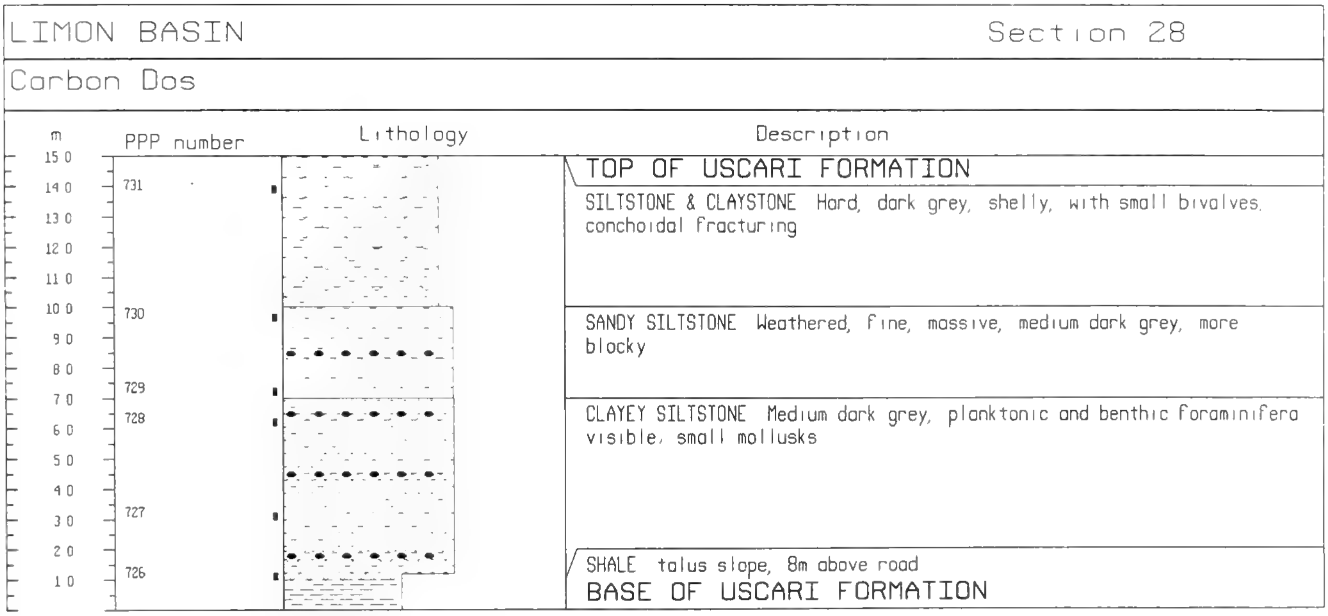
SANDY LIMESTONE Bioclastic, fine calcarenite with thick-branched corals and well stratified beds 20-50cm thick Abundant gastropods

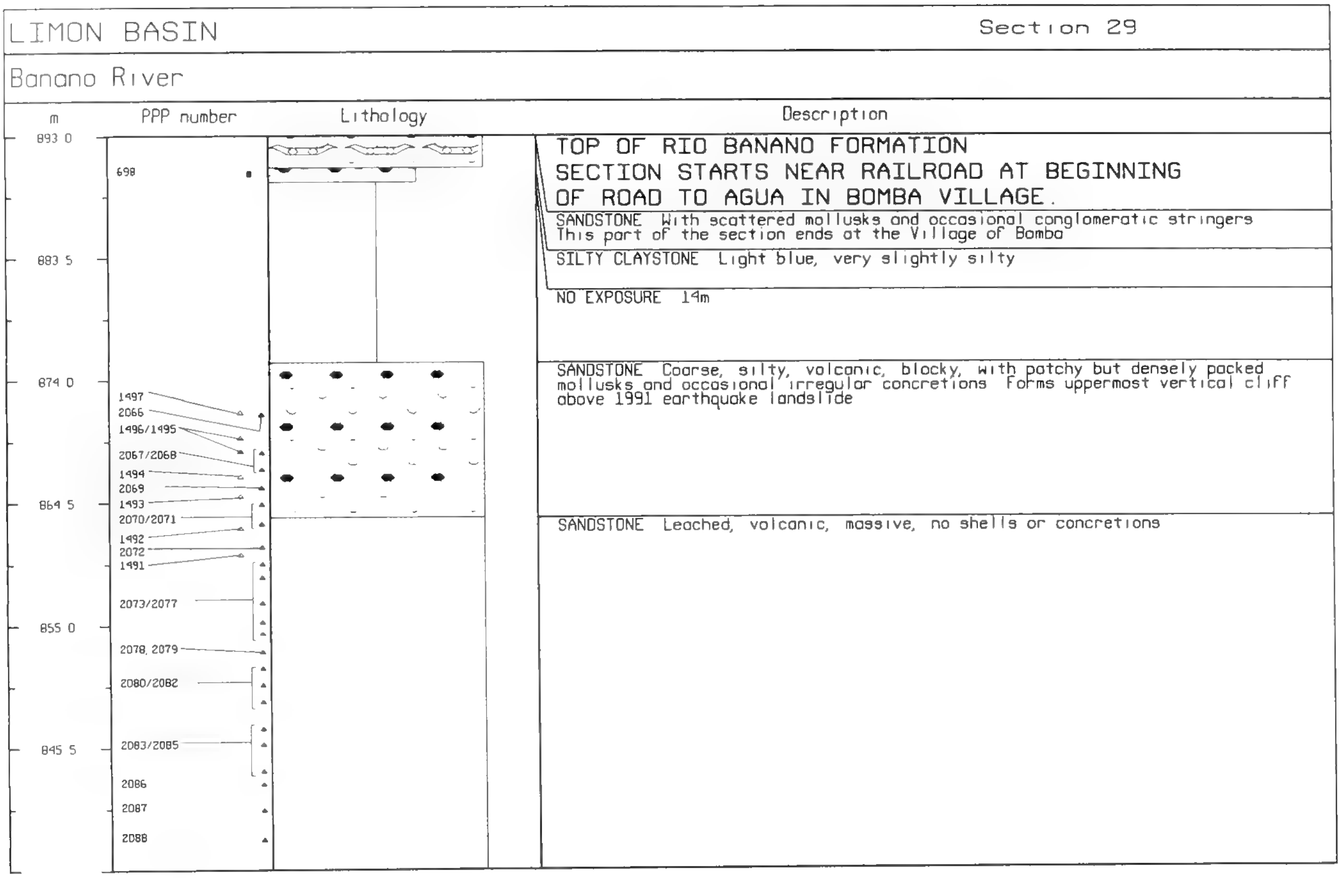
SANDY LIMESTONE Indurated, bioclastic, coarse calcarenite with thick-branched corals and discontinuous beds, dispersed mollusks

LIMESTONE Massive, coral-bearing, formed by thin-branched corals in a bioclastic mudstone matrix Light brown to cream in color

LIMESTONE Massive with thin-branching corals, very indurated, light cream in color Base of section is at sea level


LIMON BASIN
Section 27
Sandbox River
40 0
35 0
30 0
25 0
20 0
15 0
10 0
5 0
737
453/454=1989
=1736/1737
735
736
TOP OF USCARI FORMATION
SILTSTONE Massive, grey
SILTSTONE Medium, dark grey, sandy, with sparse, thin-shelled mollusks
CONGLOMERATE Rounded pebbles/cobbles, 2'-thick bed
SANDSTONE Massive, apparently unfossiliferous
CLAYEY SILTSTONE Indurated, grey
BASE OF USCARI FORMATION


LIMON BASIN
Section 28
Carbon Dos
m
PPP number
Lithology
Description
15 0
14 0
13 0
12 0
11 0
10 0
9 0
8 0
7 0
6 0
5 0
4 0
3 0
2 0
1 0
731
730
729
728
727
726
TOP OF USCARI FORMATION
SILTSTONE & CLAYSTONE Hard, dark grey, shelly, with small bivalves, conchoidal fracturing
SANDY SILTSTONE Weathered, fine, massive, medium dark grey, more blocky
CLAYEY SILTSTONE Medium dark grey, planktonic and benthic foraminifera visible, small mollusks
SHALE talus slope, 8m above road
BASE OF USCARI FORMATION



TOP OF RIO BANANO FORMATION
SECTION STARTS NEAR RAILROAD AT BEGINNING OF ROAD TO AGUA IN BOMBA VILLAGE.

SANDSTONE With scattered mollusks and occasional conglomeratic stringers This part of the section ends at the Village of Bomba

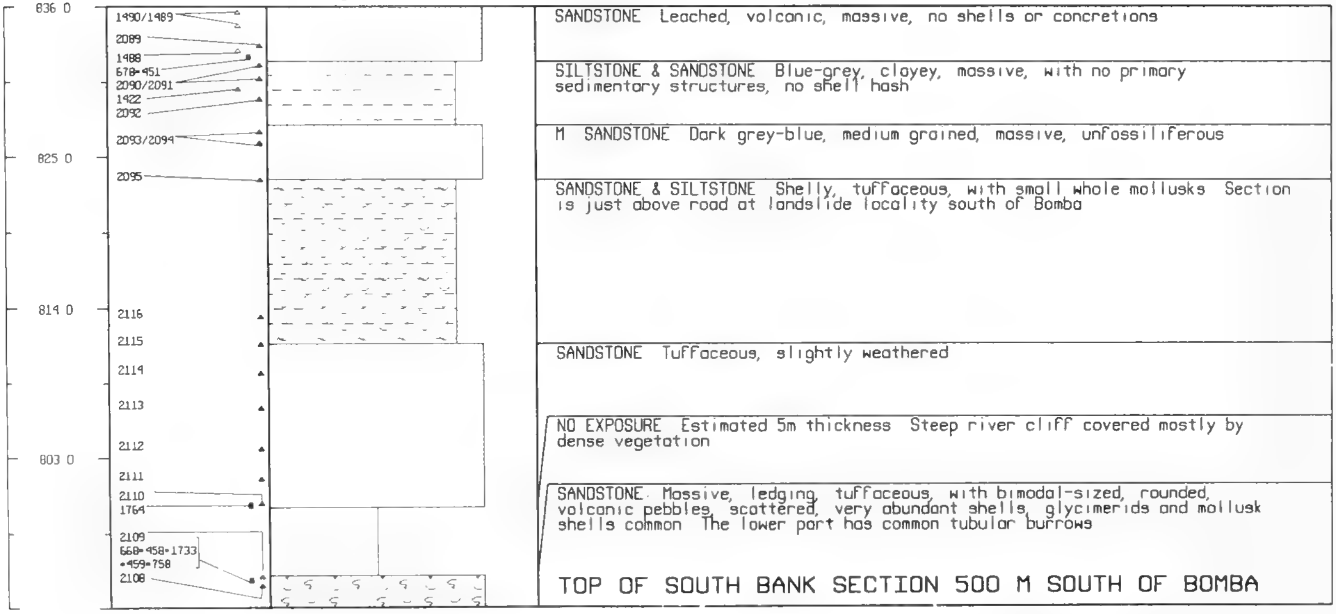
SILTY CLAYSTONE Light blue, very slightly silty

NO EXPOSURE 14m

SANDSTONE Coarse, silty, volcanic, blocky, with patchy but densely packed mollusks and occasional irregular concretions Forms uppermost vertical cliff above 1991 earthquake landslide

SANDSTONE Leached, volcanic, massive, no shells or concretions

Change of Scale



SANDSTONE Leached, volcanic, massive, no shells or concretions

SILTSTONE & SANDSTONE Blue-grey, clayey, massive, with no primary sedimentary structures, no shell hash

M SANDSTONE Dark grey-blue, medium grained, massive, unfossiliferous

SANDSTONE & SILTSTONE Shelly, tuffaceous, with small whole mollusks Section is just above road at landslide locality south of Bomba

SANDSTONE Tuffaceous, slightly weathered

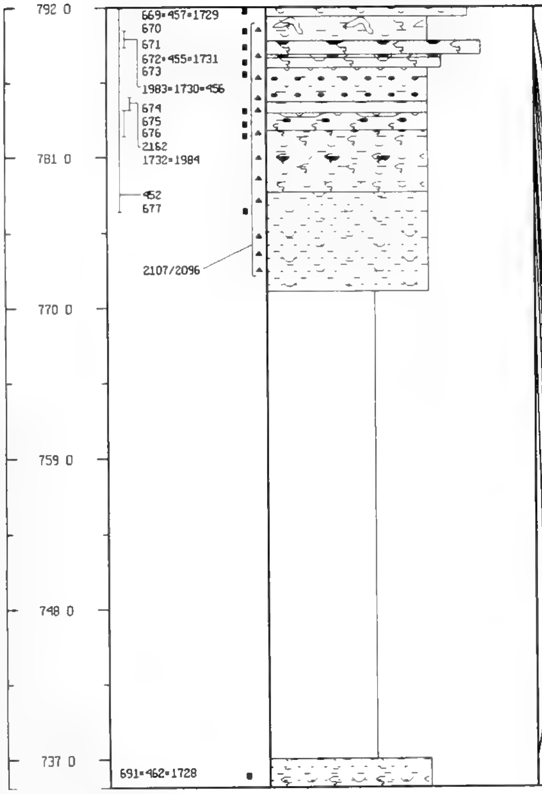
NO EXPOSURE Estimated 5m thickness Steep river cliff covered mostly by dense vegetation

SANDSTONE Massive, ledging, tuffaceous, with bimodal-sized, rounded, volcanic pebbles, scattered, very abundant shells, glycimerids and mollusk shells common The lower part has common tubular burrows

TOP OF SOUTH BANK SECTION 500 M SOUTH OF BOMBA

Change of Scale

Section 29, contd.



SANDSTONE W SILTSTONE INTERBEDS: Coarse and fine, with abundant rounded, smooth pebbles 1 cm or less, scattered *Turritella*, bivalves, and snails with common fine shell hash. The base is marked by a dense *Turritella* layer and a line of slabby concretions

SILTSTONE: Tuffaceous, with scattered volcanic pebbles. In mid unit intense callianassid-type burrows filled with more volcanic pebbles (2-4mm). A shell hash with frequent *Mellita*-like echinoids. Burrows less toward the base with lithology becoming more organic rich and tan weathering

SANDSTONE: Brownish, organic rich, volcaniclastic, with blocky ledge at top with 1-cm-vertical-diameter burrows

SILTSTONE W SANDSTONE INTERBEDS: Massive, dark brown, organic rich, tuffaceous and fine, rich in bivalves, and micromollusks. Prominent concretionary layers at base

SILTSTONE: Thick, massive, light tan-brown weathering, tuffaceous, with scattered whole mollusks but very rich in micromollusks and shell hash. Scattered 10-20-cm, rounded concretions. Bivalves common. Base is a hard, calcified layer. Upper and lower surfaces rich in mollusks. Occasional cheilostome bryozoans

SILTSTONE: Blue-grey, unfossiliferous, massive

SILTSTONE: Blue-grey, clayey, rich in mollusks (whole and shell hash), lenses 1-2"thick, 1-2" stringers with abundant *Pecten* and shell hash. Pervasive bioturbation. Concretions at base preferentially in coarse shell hash

SILTSTONE: Blue-grey, tan-brown weathering, tuffaceous with wispy, claystone layers every 10-20cm. Siltstone between is pervasively bioturbated. Evenly distributed coarse shell hash with scattered mollusks. Occasional shell nests, 8-10cm in diameter. Shell hash also in thin stringers

CLAYEY SILTSTONE: Grey-blue, clayey, massive, thick bedded, organic rich, with thin-shelled mollusks and abundant shell hash. Outcrop at river level

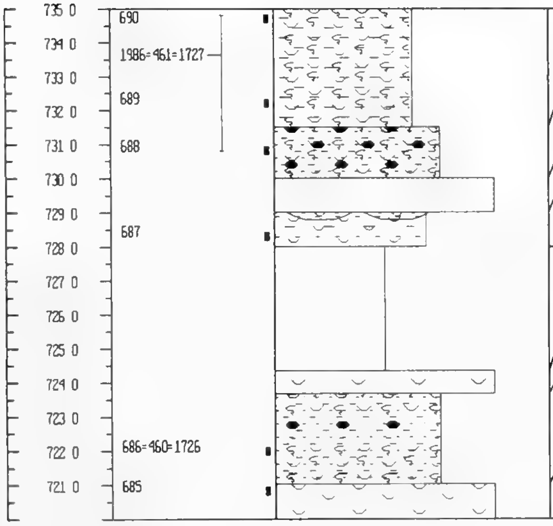
BASE OF SOUTH BANK BOMBA SECTION, 500 M. S.W. OF BOMBA.

NO EXPOSURE: 35m

CLAYEY SILTSTONE: Massive, pervasively bioturbated, rich in shell hash. Concentrated shell bed at base with arcids, intensely burrowed

TOP OF NORTH BANK SECTION 700 M SW BOMBA.

Change of Scale



CLAYSTONE: Grey, calcareous, burrow mottled, rich in small mollusks. Burrows are packed with shell hash. Whole, thin-shelled mollusks common, very fossiliferous

CLAYEY SILTSTONE: Grey, with scattered 2-5-cm volcanic pebbles, crammed with mollusks and hash, pervasive bioturbation and unoriented *Turritella*

SANDSTONE: Weathered, slightly coarse, volcanic

CLAYSTONE & SILTSTONE: Grey, finer than PPP 686. Occasional small mollusks and fine shell hash. Lenses of *Corbula* and sporadic, small *Dentalium*

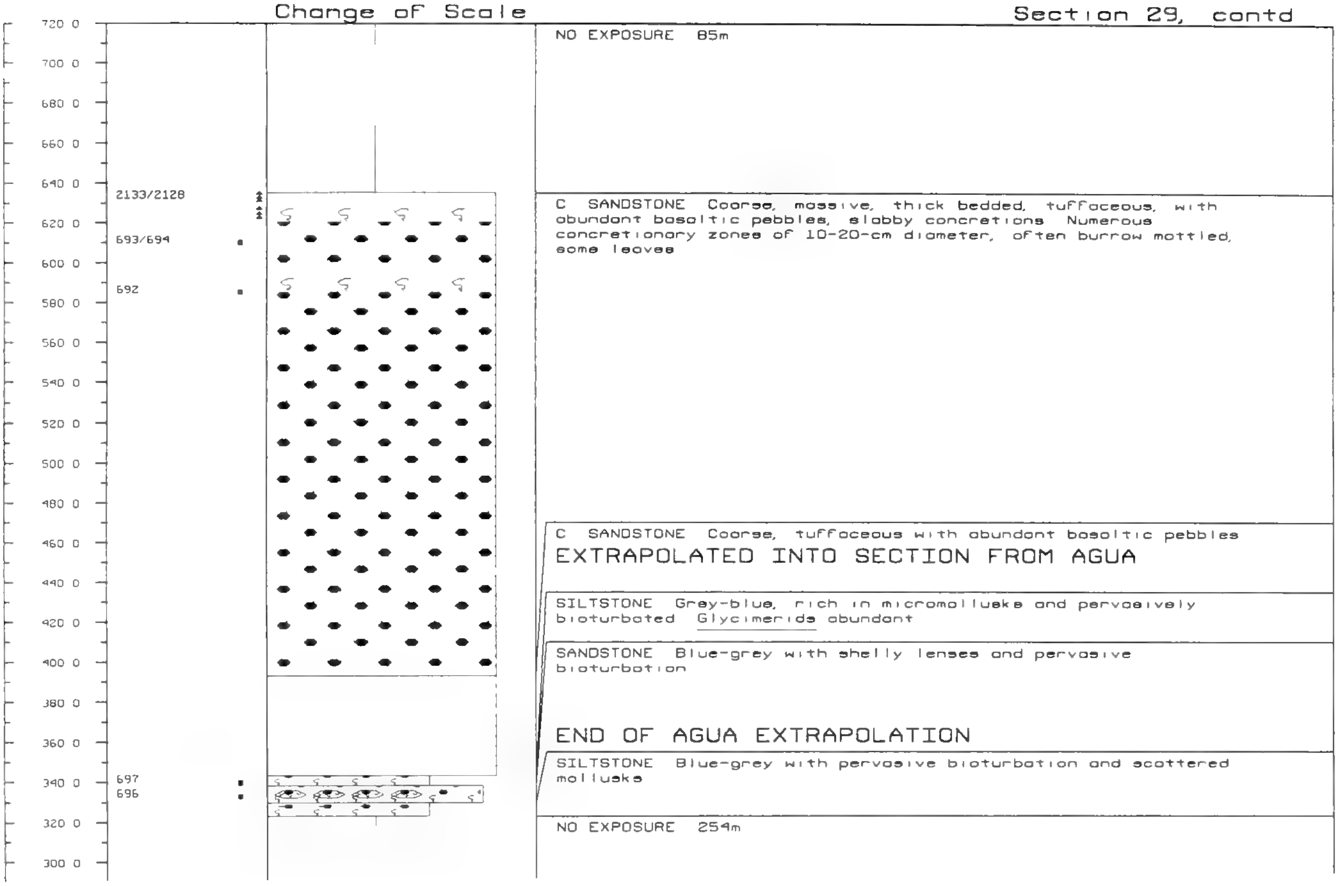
NO EXPOSURE: 3.66m

BASE OF SECTION ON NORTH BANK OF BANANO RIVER, APPROX. 600 M FROM ROAD JUNCTION IN BOMBA

SANDSTONE: Blue-grey, shelly, clayey, rich in small bivalves

CLAYEY SILTSTONE: Volcanic, pervasively bioturbated, with lenses of coarse mollusks, scattered shell hash and occasional tubular burrows. Calcareous hard bed (10 cm) with rich and well cemented bivalve surfaces

SANDSTONE: Grey-blue, medium to fine volcanic, rich in small mollusks. Occasional lenses of abundant *Corbula*



NO EXPOSURE 85m

C SANDSTONE Coarse, massive, thick bedded, tuffaceous, with abundant basaltic pebbles, slabby concretions Numerous concretionary zones of 10-20-cm diameter, often burrow mottled, some leaves

C SANDSTONE Coarse, tuffaceous with abundant basaltic pebbles

EXTRAPOLATED INTO SECTION FROM AGUA

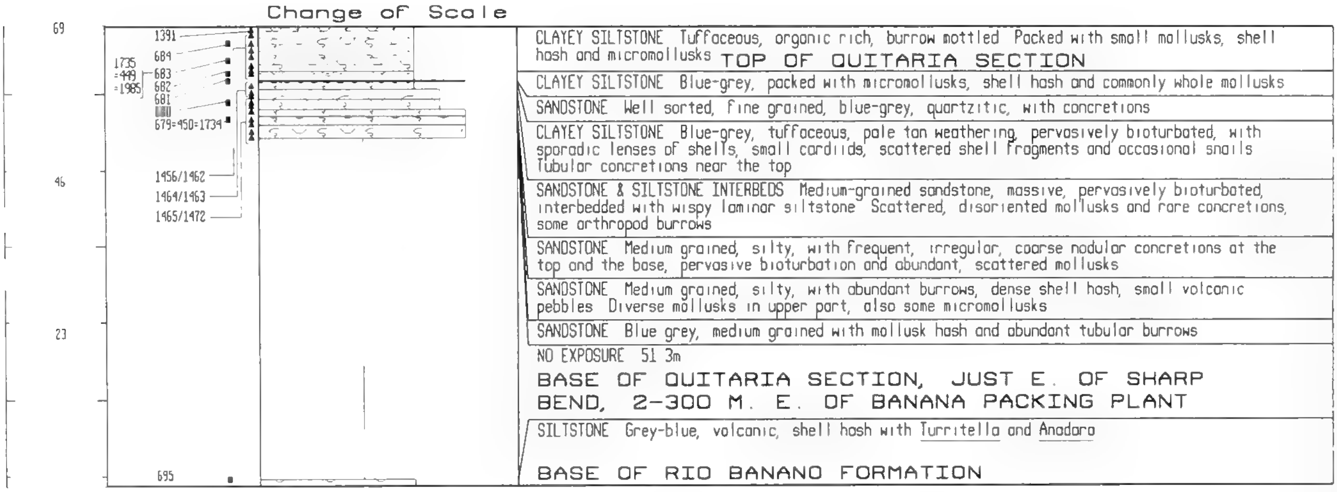
SILTSTONE Grey-blue, rich in micromollusks and pervasively bioturbated Glycimerids abundant

SANDSTONE Blue-grey with shelly lenses and pervasive bioturbation

END OF AGUA EXTRAPOLATION

SILTSTONE Blue-grey with pervasive bioturbation and scattered mollusks

NO EXPOSURE 254m



CLAYEY SILTSTONE Tuffaceous, organic rich, burrow mottled Packed with small mollusks, shell hash and micromollusks TOP OF QUITARIA SECTION

CLAYEY SILTSTONE Blue-grey, packed with micromollusks, shell hash and commonly whole mollusks

SANDSTONE Well sorted, fine grained, blue-grey, quartzitic, with concretions

CLAYEY SILTSTONE Blue-grey, tuffaceous, pale tan weathering, pervasively bioturbated, with sporadic lenses of shells, small cardiids, scattered shell fragments and occasional snails Tubular concretions near the top

SANDSTONE & SILTSTONE INTERBEDS Medium-grained sandstone, massive, pervasively bioturbated, interbedded with wispy laminar siltstone Scattered, disoriented mollusks and rare concretions, some arthropod burrows

SANDSTONE Medium grained, silty, with frequent, irregular, coarse nodular concretions at the top and the base, pervasive bioturbation and abundant, scattered mollusks

SANDSTONE Medium grained, silty, with abundant burrows, dense shell hash, small volcanic pebbles Diverse mollusks in upper part, also some micromollusks

SANDSTONE Blue grey, medium grained with mollusk hash and abundant tubular burrows

NO EXPOSURE 51 3m

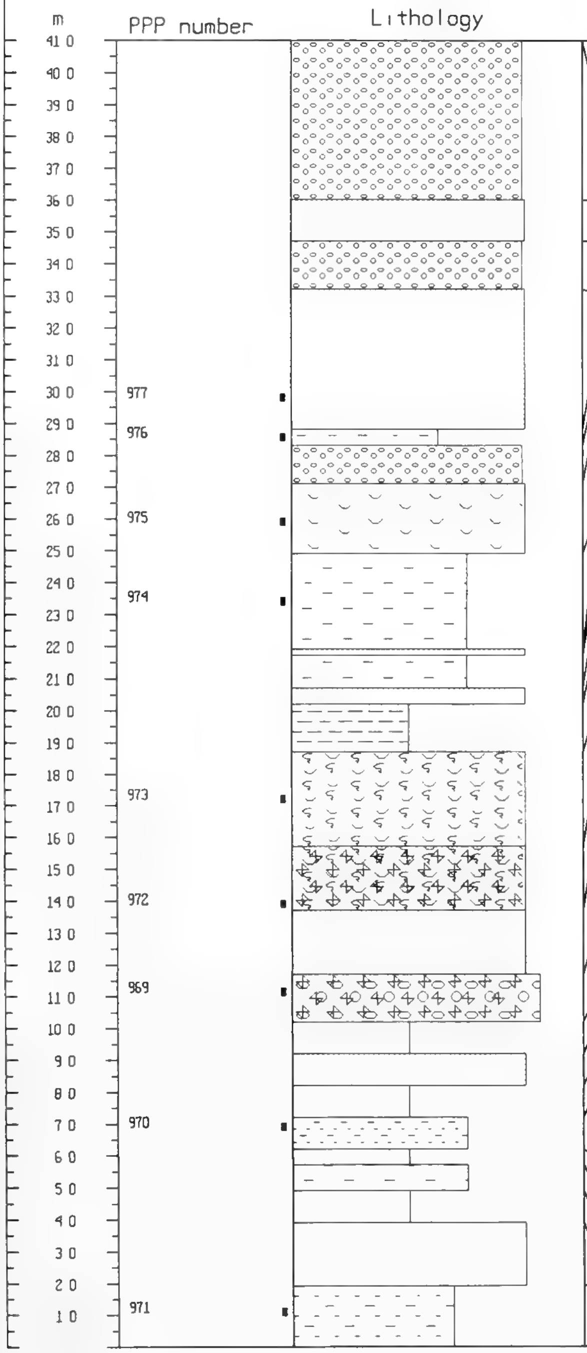
BASE OF QUITARIA SECTION, JUST E. OF SHARP BEND, 2-300 M. E. OF BANANA PACKING PLANT

SILTSTONE Grey-blue, volcanic, shell hash with Turritella and Anadara

BASE OF RIO BANANO FORMATION

LIMON BASIN Section 30

Peje River



Description

TOP OF RIO BANANO FORMATION

CONGLOMERATE Massive, poorly sorted, volcanic Rounded cobbles

SANDSTONE Bright blue, sandy matrix, scattered cobbles to 6 cm

CONGLOMERATE: Cobbles to 6 cm, rounded, very poorly sorted, all sizes to clay

SANDSTONE: Massive, fine-medium, clayey, leached No structure or fossils

CLAYSTONE

CONGLOMERATE: Well rounded volcanic cobbles, graded at top

SANDSTONE Volcanic, low diversity nested shell bed, densely packed bivalves, medium thick, encrusting bryozoa, ledging unit wavy bedded claystone channels at top

SILTSTONE

SANDSTONE: Medium fine, volcanic

SILTSTONE

SANDSTONE

SANDY SHALE: With shelly material Estuarine facies? Rip up clasts at base

SANDSTONE: Fine, massive ledging, with dispersed shells and poorly defined burrows

SANDSTONE Fine medium, fragments of shells and wood, dispersed shells *Corbula* Shell filled burrows

SANDSTONE: Massive, blue-grey volcanic, grading coarser, unfossiliferous

CONGLOMERATIC SANDSTONE: Volcanic, abundant large seeds and wood

NO EXPOSURE: 1 m

SANDSTONE: Medium, laminated, well sorted

NO EXPOSURE: 1 m

CLAYEY SILTSTONE: Thin sandstone, ledging unit with blocks of silty clay

NO EXPOSURE: 1 m

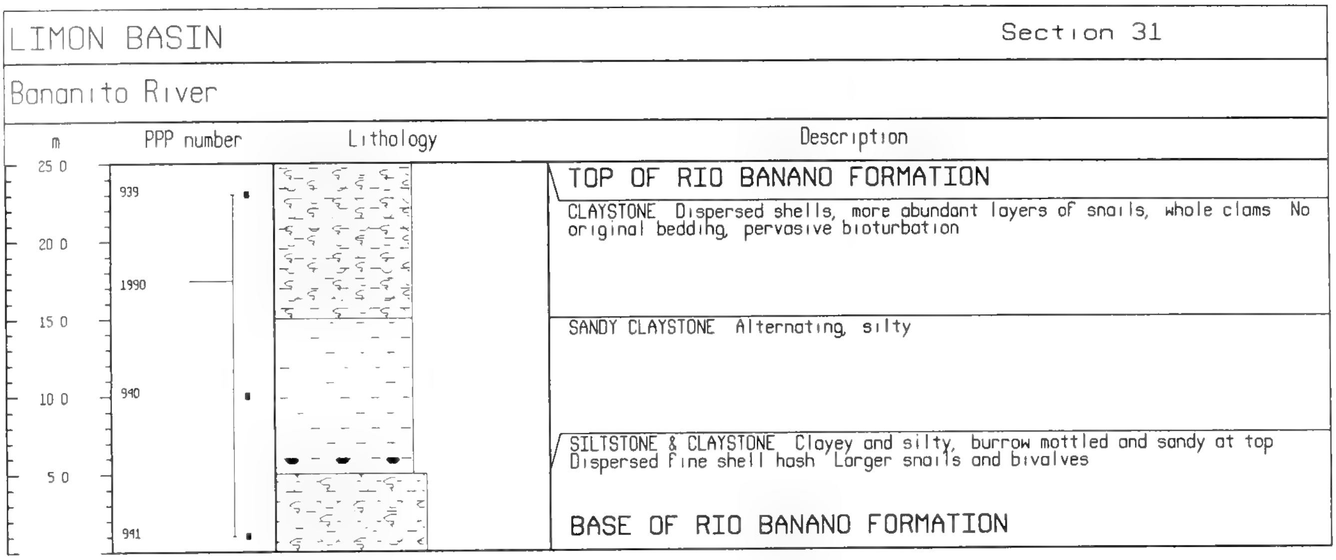
SILTSTONE: Blocky, leached, no fossils

NO EXPOSURE 1 m

SANDSTONE Medium-fine, well sorted, volcanic, grading to siltstone

SILTSTONE & CLAYSTONE

BASE OF RIO BANANO FORMATION



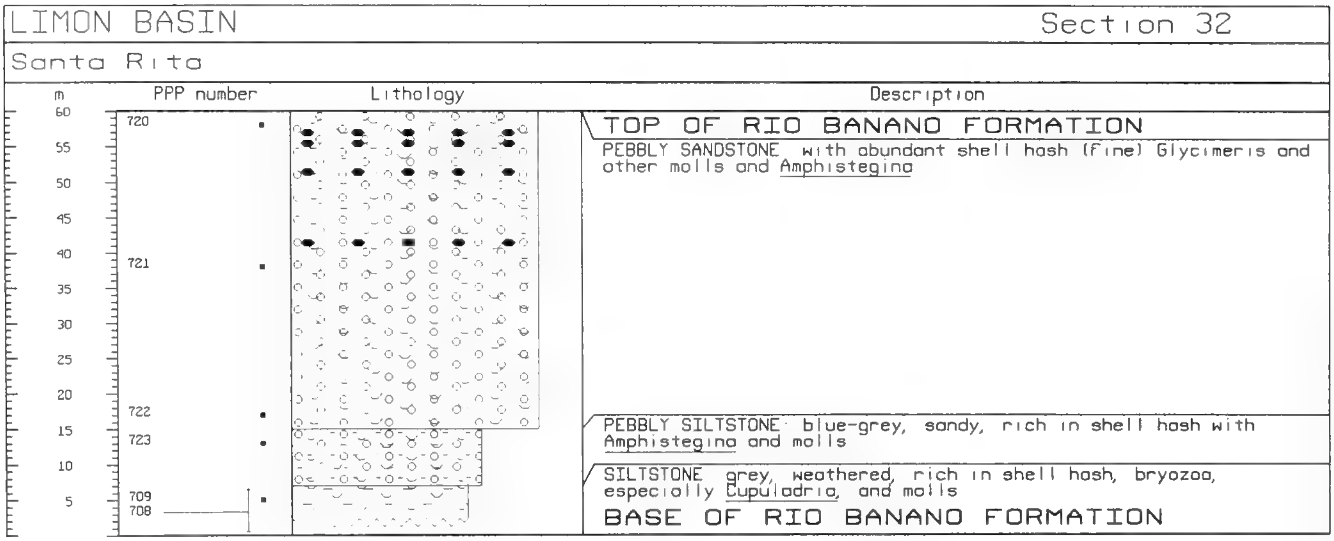
TOP OF RIO BANANO FORMATION

CLAYSTONE Dispersed shells, more abundant layers of snails, whole clams No original bedding, pervasive bioturbation

SANDY CLAYSTONE Alternating, silty

SILTSTONE & CLAYSTONE Clayey and silty, burrow mottled and sandy at top Dispersed fine shell hash Larger snails and bivalves

BASE OF RIO BANANO FORMATION



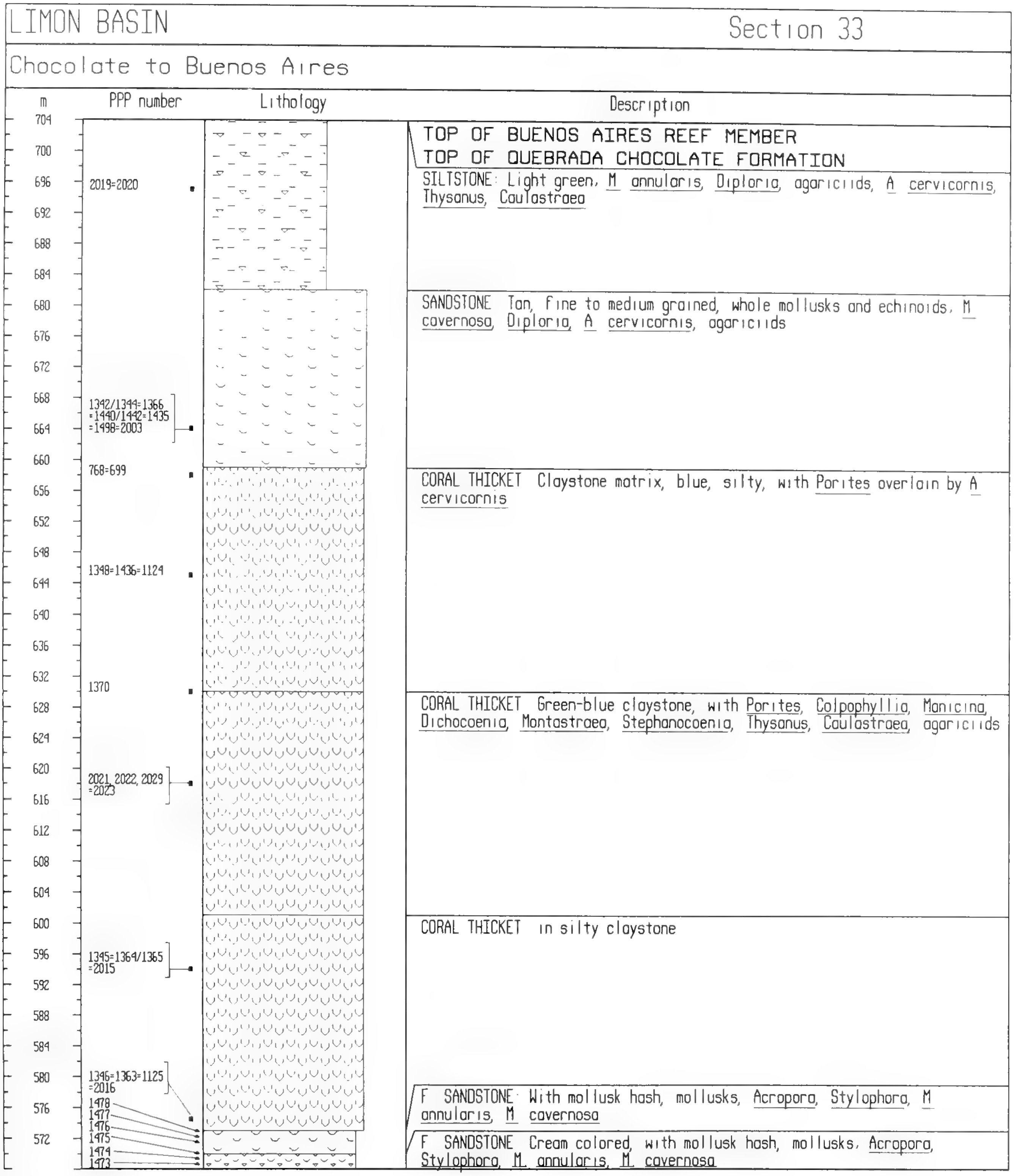
TOP OF RIO BANANO FORMATION

PEBBLY SANDSTONE with abundant shell hash (fine) Glycimeris and other molls and *Amphistegina*

PEBBLY SILTSTONE blue-grey, sandy, rich in shell hash with *Amphistegina* and molls

SILTSTONE grey, weathered, rich in shell hash, bryozoa, especially *Cupuladria*, and molls

BASE OF RIO BANANO FORMATION



LIMON BASIN

Section 33

Chocolate to Buenos Aires

TOP OF BUENOS AIRES REEF MEMBER
TOP OF QUEBRADA CHOCOLATE FORMATION

SILTSTONE: Light green, M annularis, Diploria, agariciids, A cervicornis, Thysanus, Caulastraea

SANDSTONE Tan, fine to medium grained, whole mollusks and echinoids, M cavernosa, Diploria, A cervicornis, agariciids

CORAL THICKET Claystone matrix, blue, silty, with Porites overlain by A cervicornis

CORAL THICKET Green-blue claystone, with Porites, Colpophyllia, Manicina, Dichocoenia, Montastraea, Stephanocoenia, Thysanus, Caulastraea, agariciids

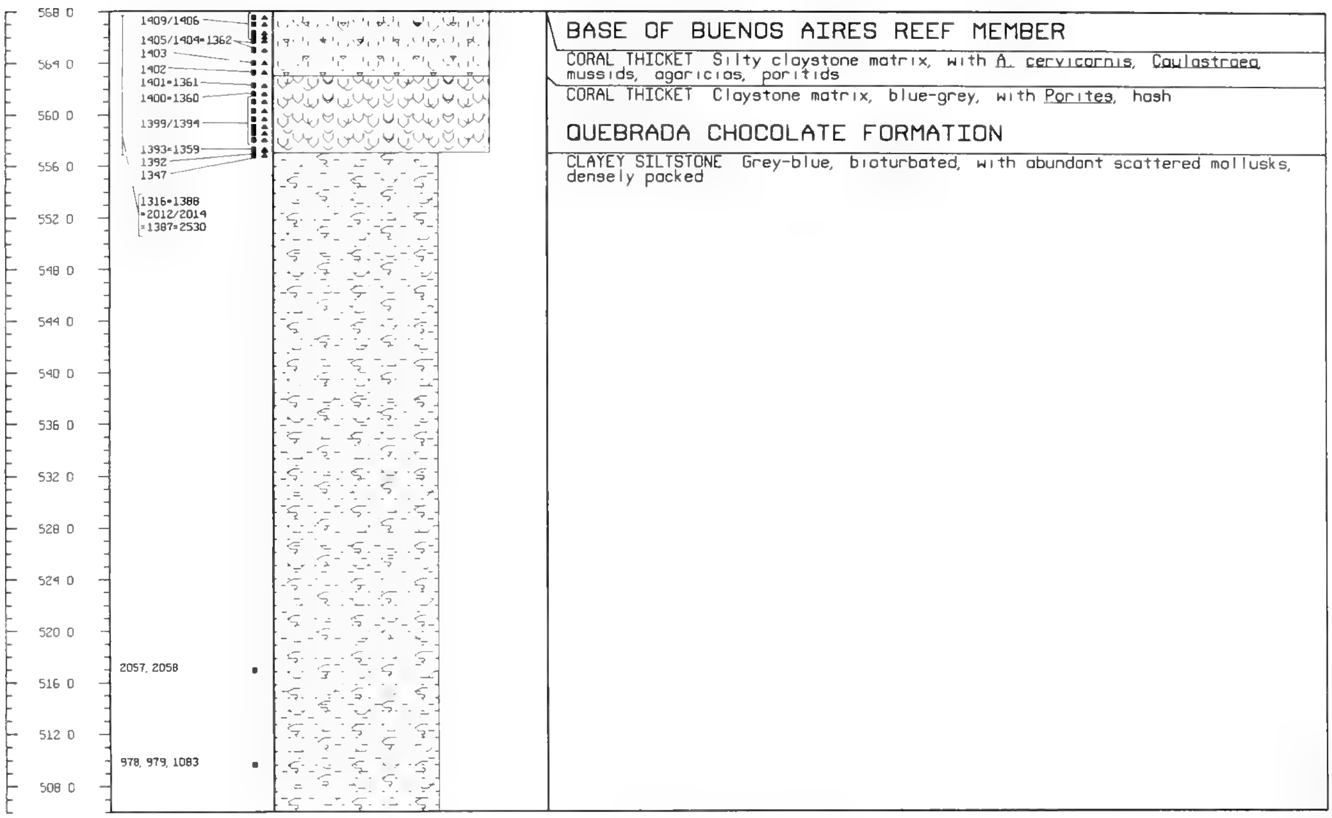
CORAL THICKET in silty claystone

F SANDSTONE: With mollusk hash, mollusks, Acropora, Stylophora, M annularis, M cavernosa

F SANDSTONE Cream colored, with mollusk hash, mollusks, Acropora, Stylophora, M annularis, M cavernosa

Change of Scale

Section 33, contd.



BASE OF BUENOS AIRES REEF MEMBER

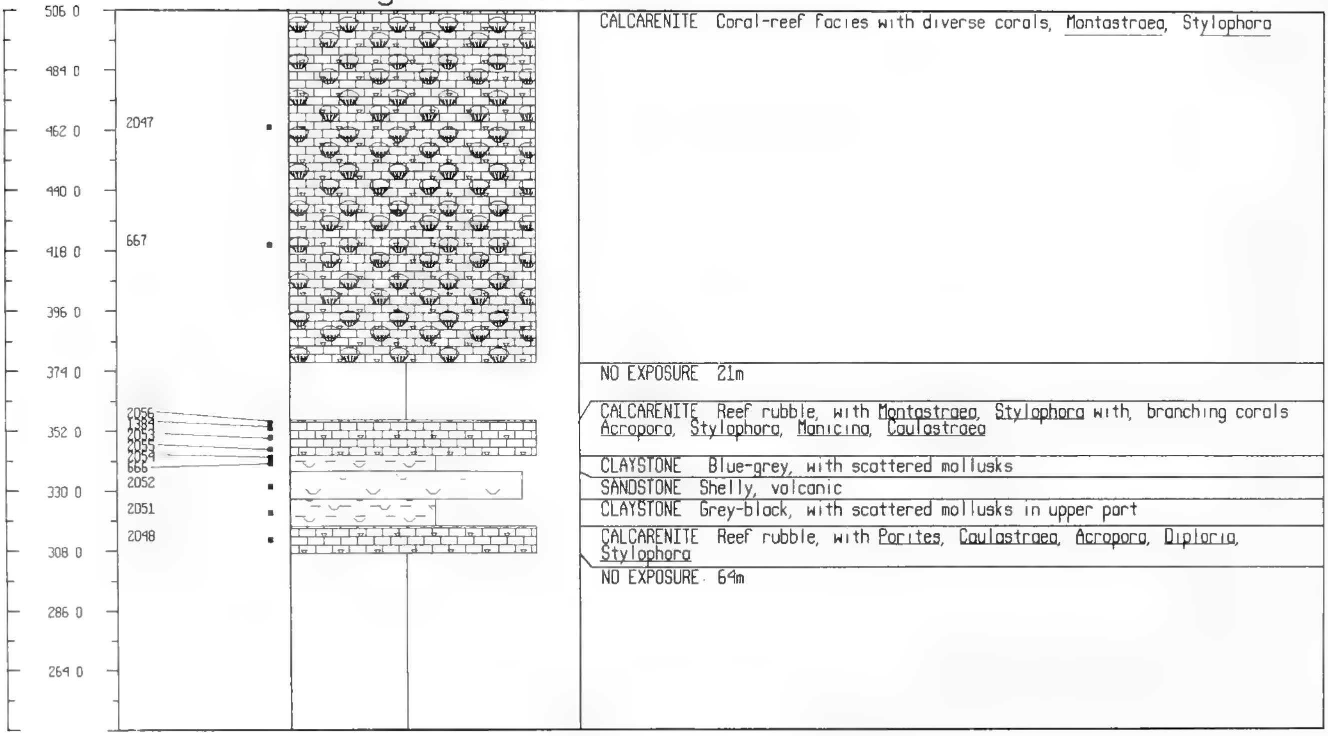
CORAL THICKET Silty claystone matrix, with _A. cervicornis_, _Caulastraea_, mussids, agaricias, poritids

CORAL THICKET Claystone matrix, blue-grey, with _Porites_, hash

QUEBRADA CHOCOLATE FORMATION

CLAYEY SILTSTONE Grey-blue, bioturbated, with abundant scattered mollusks, densely packed

Change of Scale



CALCARENITE Coral-reef facies with diverse corals, _Montastraea_, _Stylophora_

NO EXPOSURE 21m

CALCARENITE Reef rubble, with _Montastraea_, _Stylophora_ with, branching corals _Acropora_, _Stylophora_, _Manicina_, _Caulastraea_

CLAYSTONE Blue-grey, with scattered mollusks

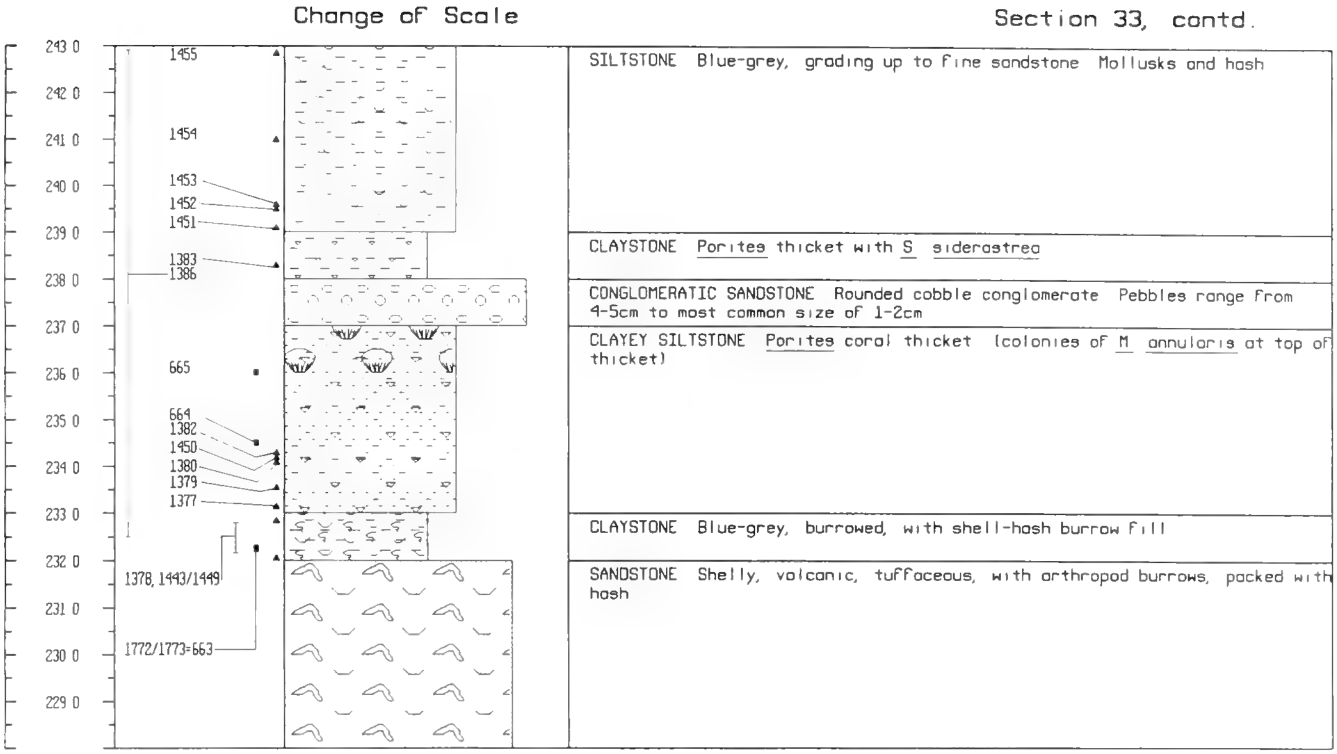
SANDSTONE Shelly, volcanic

CLAYSTONE Grey-black, with scattered mollusks in upper part

CALCARENITE Reef rubble, with _Porites_, _Caulastraea_, _Acropora_, _Diploria_, _Stylophora_

NO EXPOSURE 64m

## Section 33, contd.



SILTSTONE Blue-grey, grading up to fine sandstone Mollusks and hash

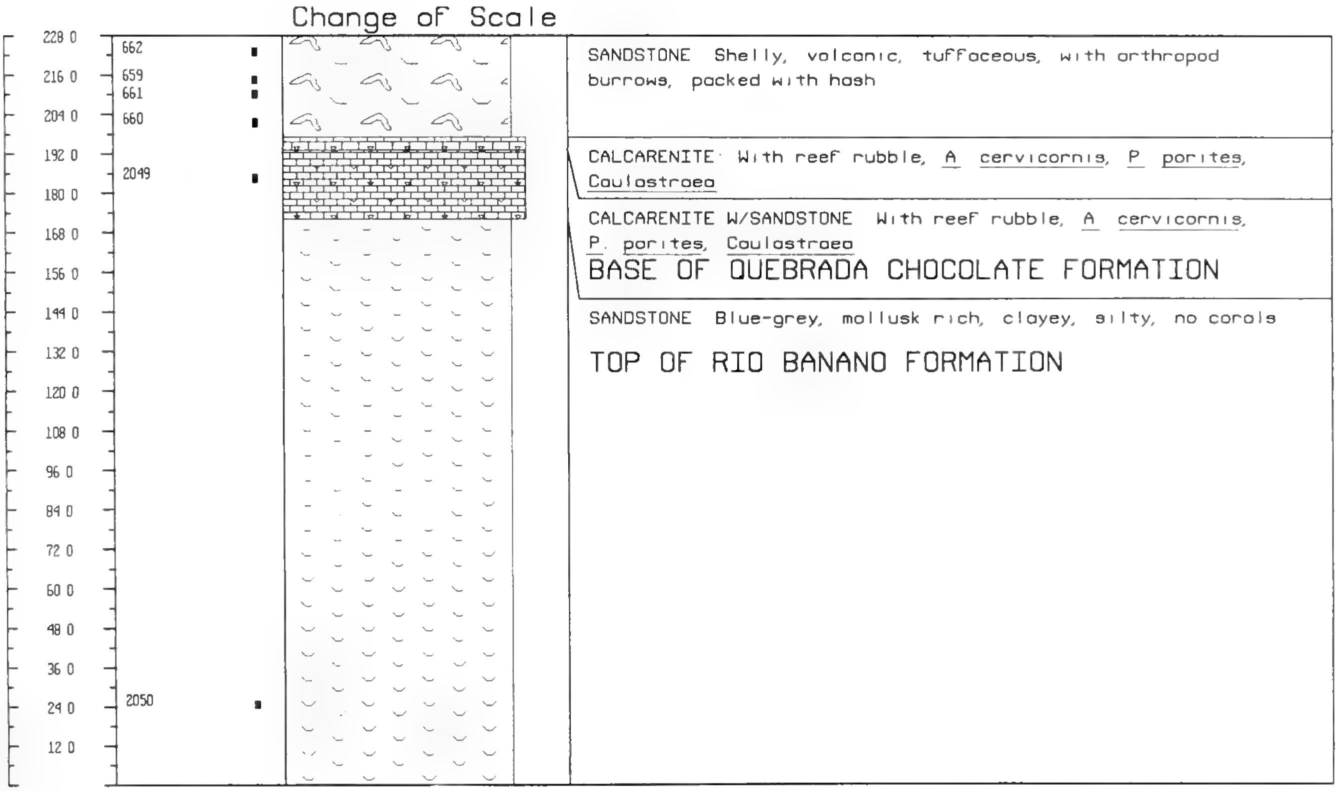
CLAYSTONE *Porites* thicket with *S siderastrea*

CONGLOMERATIC SANDSTONE Rounded cobble conglomerate Pebbles range from 4-5cm to most common size of 1-2cm

CLAYEY SILTSTONE *Porites* coral thicket (colonies of *M annularis* at top of thicket)

CLAYSTONE Blue-grey, burrowed, with shell-hash burrow fill

SANDSTONE Shelly, volcanic, tuffaceous, with orthropod burrows, packed with hash



SANDSTONE Shelly, volcanic, tuffaceous, with orthropod burrows, packed with hash

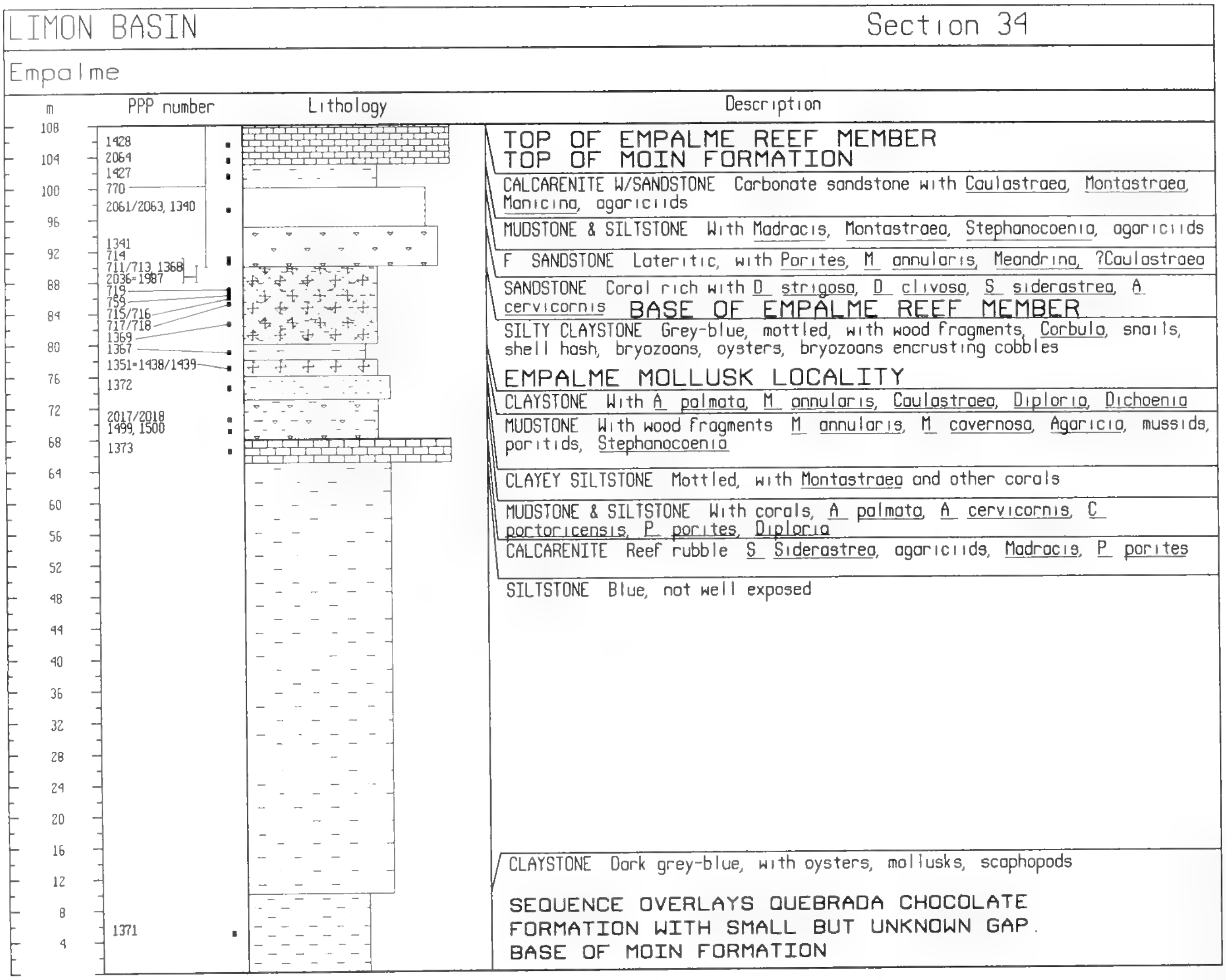
CALCARENITE With reef rubble, *A cervicornis*, *P porites*, *Coulostraea*

CALCARENITE W/SANDSTONE With reef rubble, *A cervicornis*, *P. porites*, *Coulostraea*

BASE OF QUEBRADA CHOCOLATE FORMATION

SANDSTONE Blue-grey, mollusk rich, clayey, silty, no corals

TOP OF RIO BANANO FORMATION



TOP OF EMPALME REEF MEMBER
TOP OF MOIN FORMATION

CALCARENITE W/SANDSTONE Carbonate sandstone with *Caulastraea*, *Montastraea*, *Manicina*, agariciids

MUDSTONE & SILTSTONE With *Madracis*, *Montastraea*, *Stephanocoenia*, agariciids

F SANDSTONE Lateritic, with *Porites*, *M annularis*, *Meandrina*, ?*Caulastraea*

SANDSTONE Coral rich with *D strigosa*, *D clivosa*, *S siderastrea*, *A cervicornis* BASE OF EMPALME REEF MEMBER

SILTY CLAYSTONE Grey-blue, mottled, with wood fragments, *Corbula*, snails, shell hash, bryozoans, oysters, bryozoans encrusting cobbles

EMPALME MOLLUSK LOCALITY

CLAYSTONE With *A palmata*, *M annularis*, *Caulastraea*, *Diploria*, *Dichoenia*

MUDSTONE With wood fragments *M annularis*, *M cavernosa*, *Agaricia*, mussids, poritids, *Stephanocoenia*

CLAYEY SILTSTONE Mottled, with *Montastraea* and other corals

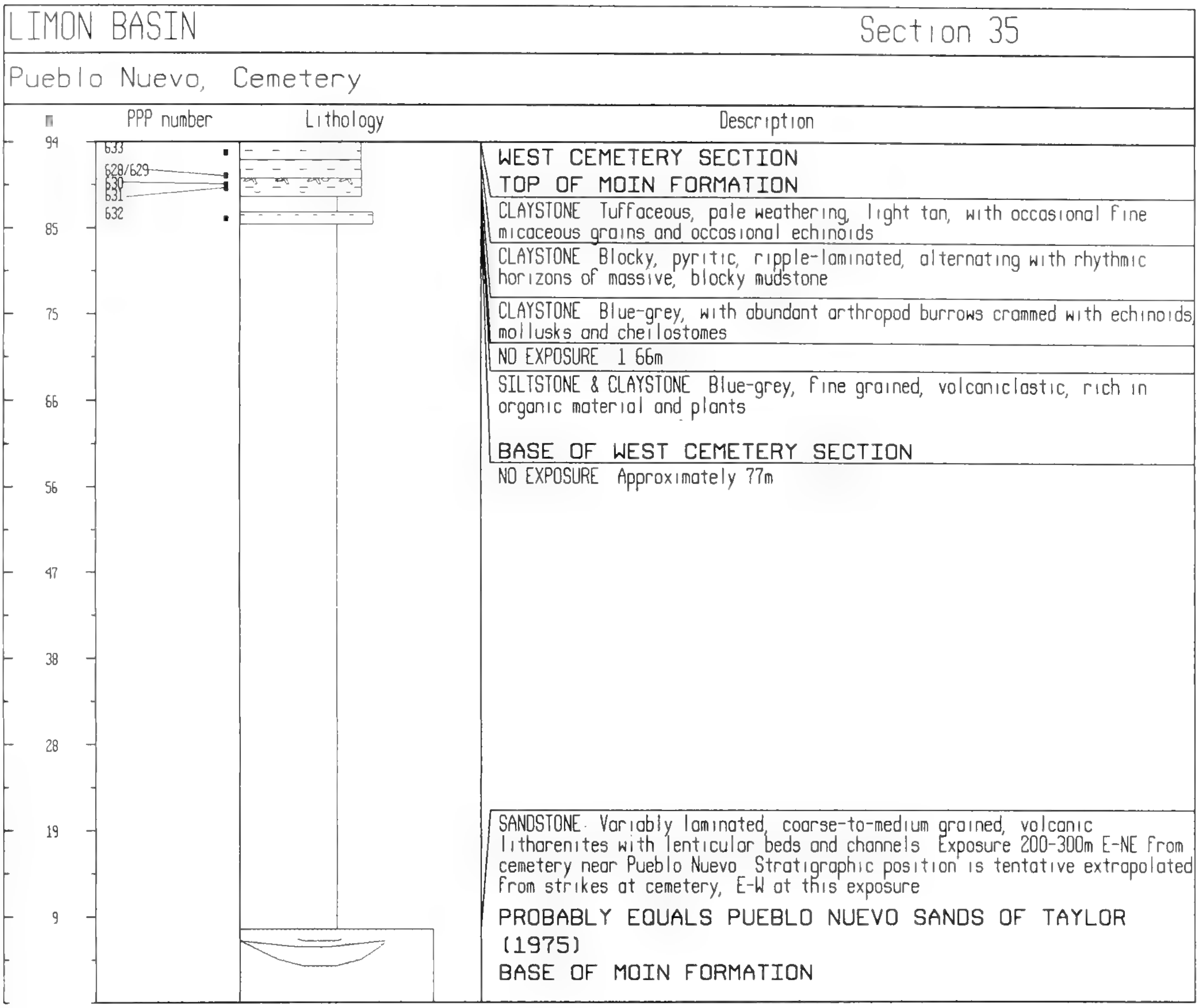
MUDSTONE & SILTSTONE With corals, *A palmata*, *A cervicornis*, *C portoricensis*, *P porites*, *Diploria*

CALCARENITE Reef rubble *S Siderastrea*, agariciids, *Madracis*, *P porites*

SILTSTONE Blue, not well exposed

CLAYSTONE Dark grey-blue, with oysters, mollusks, scaphopods

SEQUENCE OVERLAYS QUEBRADA CHOCOLATE FORMATION WITH SMALL BUT UNKNOWN GAP.
BASE OF MOIN FORMATION



LIMON BASIN

Section 35

Pueblo Nuevo, Cemetery

WEST CEMETERY SECTION

TOP OF MOIN FORMATION

CLAYSTONE Tuffaceous, pale weathering, light tan, with occasional fine micaceous grains and occasional echinoids

CLAYSTONE Blocky, pyritic, ripple-laminated, alternating with rhythmic horizons of massive, blocky mudstone

CLAYSTONE Blue-grey, with abundant arthropod burrows crammed with echinoids, mollusks and cheilostomes

NO EXPOSURE 1 66m

SILTSTONE & CLAYSTONE Blue-grey, fine grained, volcaniclastic, rich in organic material and plants

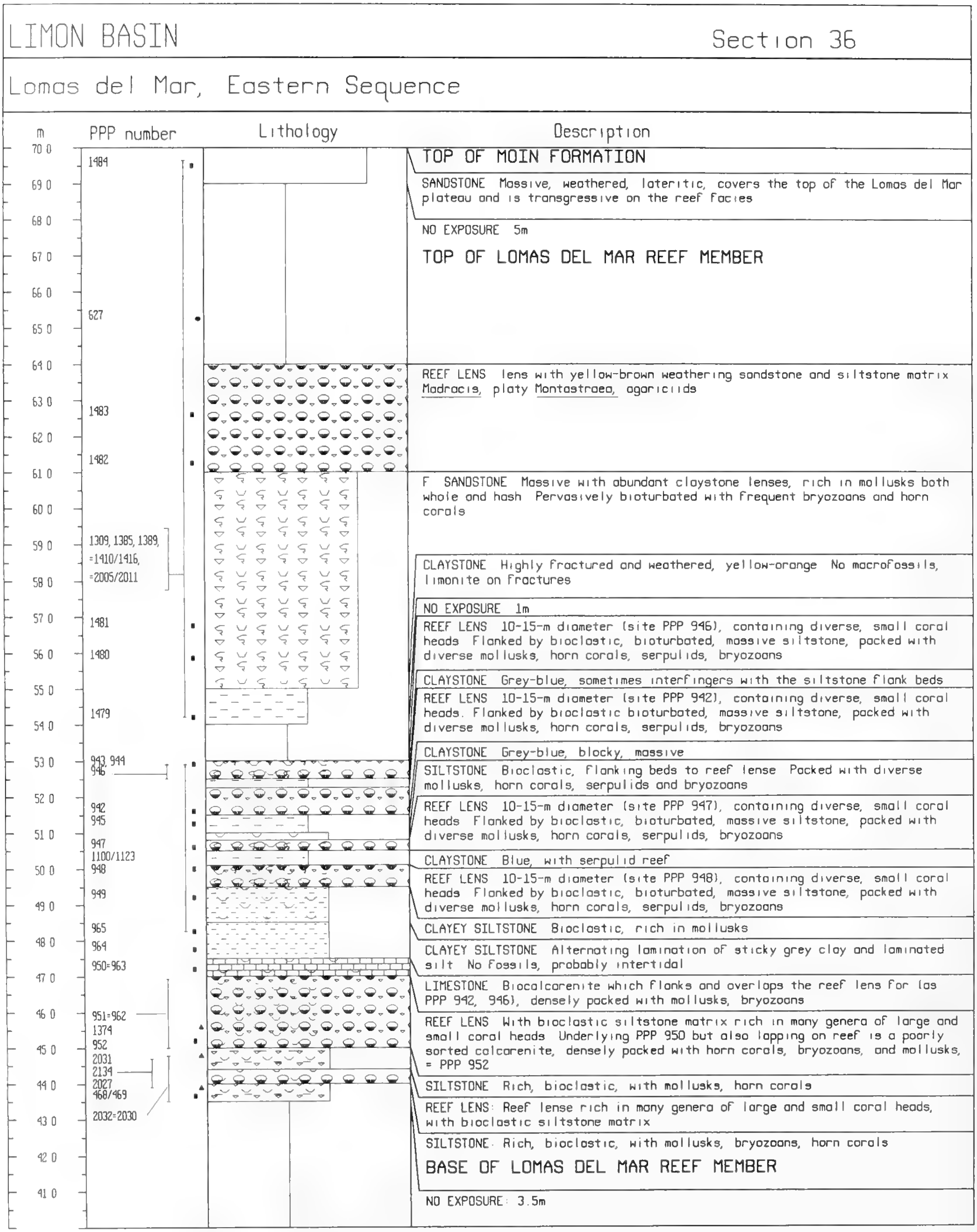
BASE OF WEST CEMETERY SECTION

NO EXPOSURE Approximately 77m

SANDSTONE Variably laminated, coarse-to-medium grained, volcanic litharenites with lenticular beds and channels Exposure 200-300m E-NE from cemetery near Pueblo Nuevo Stratigraphic position is tentative extrapolated from strikes at cemetery, E-W at this exposure

PROBABLY EQUALS PUEBLO NUEVO SANDS OF TAYLOR (1975)

BASE OF MOIN FORMATION



LIMON BASIN Section 36

Lomas del Mar, Eastern Sequence

TOP OF MOIN FORMATION

SANDSTONE Massive, weathered, lateritic, covers the top of the Lomas del Mar plateau and is transgressive on the reef facies

NO EXPOSURE 5m

TOP OF LOMAS DEL MAR REEF MEMBER

REEF LENS lens with yellow-brown weathering sandstone and siltstone matrix <u>Madracis</u>, platy <u>Montastraea</u>, agariciids

F SANDSTONE Massive with abundant claystone lenses, rich in mollusks both whole and hash Pervasively bioturbated with frequent bryozoans and horn corals

CLAYSTONE Highly fractured and weathered, yellow-orange No macrofossils, limonite on fractures

NO EXPOSURE 1m

REEF LENS 10-15-m diameter (site PPP 946), containing diverse, small coral heads Flanked by bioclastic, bioturbated, massive siltstone, packed with diverse mollusks, horn corals, serpulids, bryozoans

CLAYSTONE Grey-blue, sometimes interfingers with the siltstone flank beds

REEF LENS 10-15-m diameter (site PPP 942), containing diverse, small coral heads. Flanked by bioclastic bioturbated, massive siltstone, packed with diverse mollusks, horn corals, serpulids, bryozoans

CLAYSTONE Grey-blue, blocky, massive

SILTSTONE Bioclastic, flanking beds to reef lense Packed with diverse mollusks, horn corals, serpulids and bryozoans

REEF LENS 10-15-m diameter (site PPP 947), containing diverse, small coral heads Flanked by bioclastic, bioturbated, massive siltstone, packed with diverse mollusks, horn corals, serpulids, bryozoans

CLAYSTONE Blue, with serpulid reef

REEF LENS 10-15-m diameter (site PPP 948), containing diverse, small coral heads Flanked by bioclastic, bioturbated, massive siltstone, packed with diverse mollusks, horn corals, serpulids, bryozoans

CLAYEY SILTSTONE Bioclastic, rich in mollusks

CLAYEY SILTSTONE Alternating lamination of sticky grey clay and laminated silt No fossils, probably intertidal

LIMESTONE Biocalcarenite which flanks and overlaps the reef lens for (as PPP 942, 946), densely packed with mollusks, bryozoans

REEF LENS With bioclastic siltstone matrix rich in many genera of large and small coral heads Underlying PPP 950 but also lapping on reef is a poorly sorted calcarenite, densely packed with horn corals, bryozoans, and mollusks, = PPP 952

SILTSTONE Rich, bioclastic, with mollusks, horn corals

REEF LENS: Reef lense rich in many genera of large and small coral heads, with bioclastic siltstone matrix

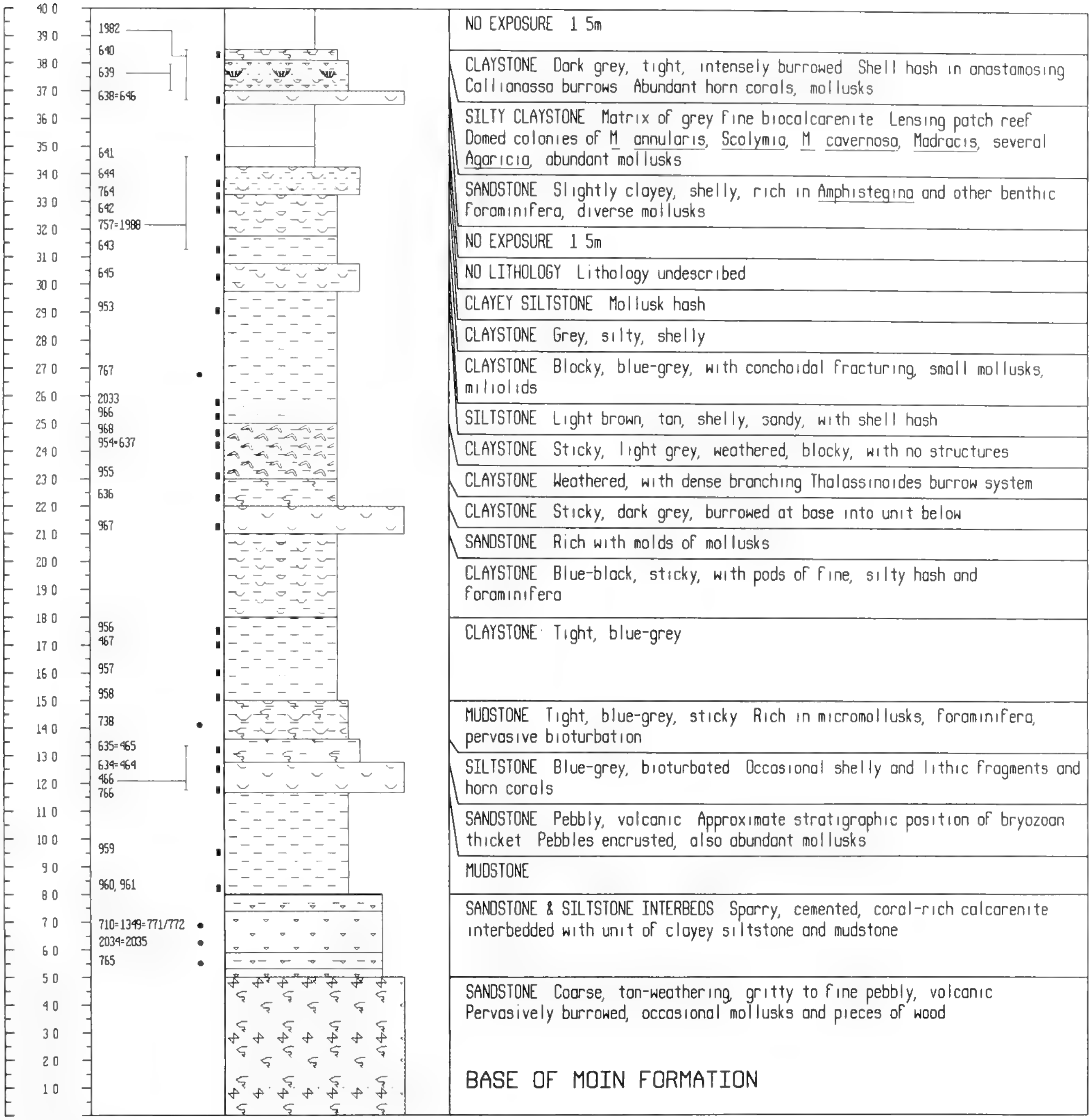
SILTSTONE: Rich, bioclastic, with mollusks, bryozoans, horn corals

BASE OF LOMAS DEL MAR REEF MEMBER

NO EXPOSURE: 3.5m

Change of Scale

Section 36, contd



NO EXPOSURE 1 5m

CLAYSTONE Dark grey, tight, intensely burrowed Shell hash in anastomosing Callianassa burrows Abundant horn corals, mollusks

SILTY CLAYSTONE Matrix of grey fine biocalcarenite Lensing patch reef Domed colonies of M annularis, Scolymia, M cavernosa, Madracis, several Agaricia, abundant mollusks

SANDSTONE Slightly clayey, shelly, rich in Amphistegina and other benthic Foraminifera, diverse mollusks

NO EXPOSURE 1 5m

NO LITHOLOGY Lithology undescribed

CLAYEY SILTSTONE Mollusk hash

CLAYSTONE Grey, silty, shelly

CLAYSTONE Blocky, blue-grey, with conchoidal fracturing, small mollusks, miliolids

SILTSTONE Light brown, tan, shelly, sandy, with shell hash

CLAYSTONE Sticky, light grey, weathered, blocky, with no structures

CLAYSTONE Weathered, with dense branching Thalassinoides burrow system

CLAYSTONE Sticky, dark grey, burrowed at base into unit below

SANDSTONE Rich with molds of mollusks

CLAYSTONE Blue-black, sticky, with pods of fine, silty hash and foraminifera

CLAYSTONE Tight, blue-grey

MUDSTONE Tight, blue-grey, sticky Rich in micromollusks, foraminifera, pervasive bioturbation

SILTSTONE Blue-grey, bioturbated Occasional shelly and lithic fragments and horn corals

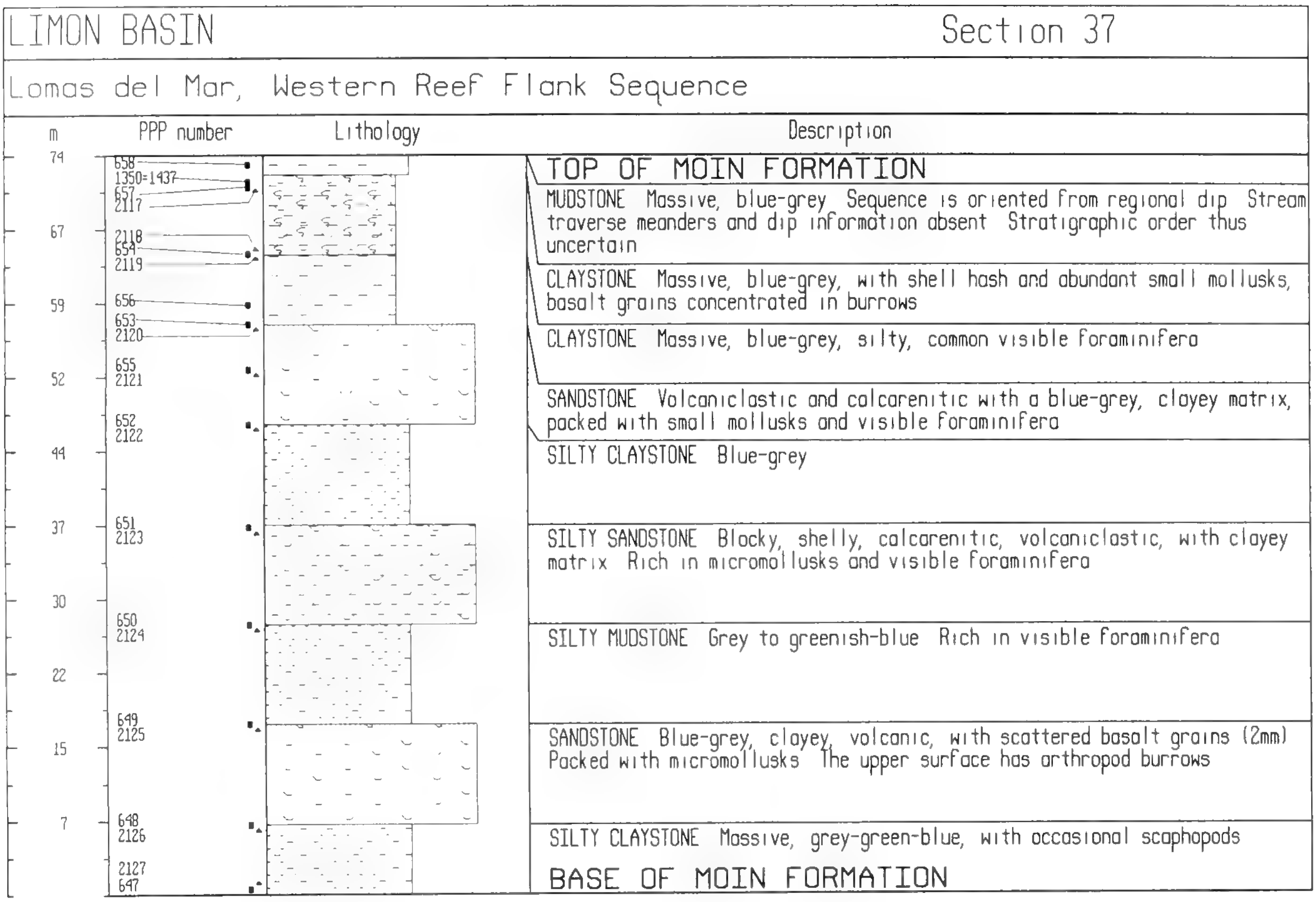
SANDSTONE Pebbly, volcanic Approximate stratigraphic position of bryozoan thicket Pebbles encrusted, also abundant mollusks

MUDSTONE

SANDSTONE & SILTSTONE INTERBEDS Sparry, cemented, coral-rich calcarenite interbedded with unit of clayey siltstone and mudstone

SANDSTONE Coarse, tan-weathering, gritty to fine pebbly, volcanic Pervasively burrowed, occasional mollusks and pieces of wood

BASE OF MOIN FORMATION



TOP OF MOIN FORMATION

MUDSTONE Massive, blue-grey Sequence is oriented from regional dip Stream traverse meanders and dip information absent Stratigraphic order thus uncertain

CLAYSTONE Massive, blue-grey, with shell hash and abundant small mollusks, basalt grains concentrated in burrows

CLAYSTONE Massive, blue-grey, silty, common visible foraminifera

SANDSTONE Volcaniclastic and calcarenitic with a blue-grey, clayey matrix, packed with small mollusks and visible foraminifera

SILTY CLAYSTONE Blue-grey

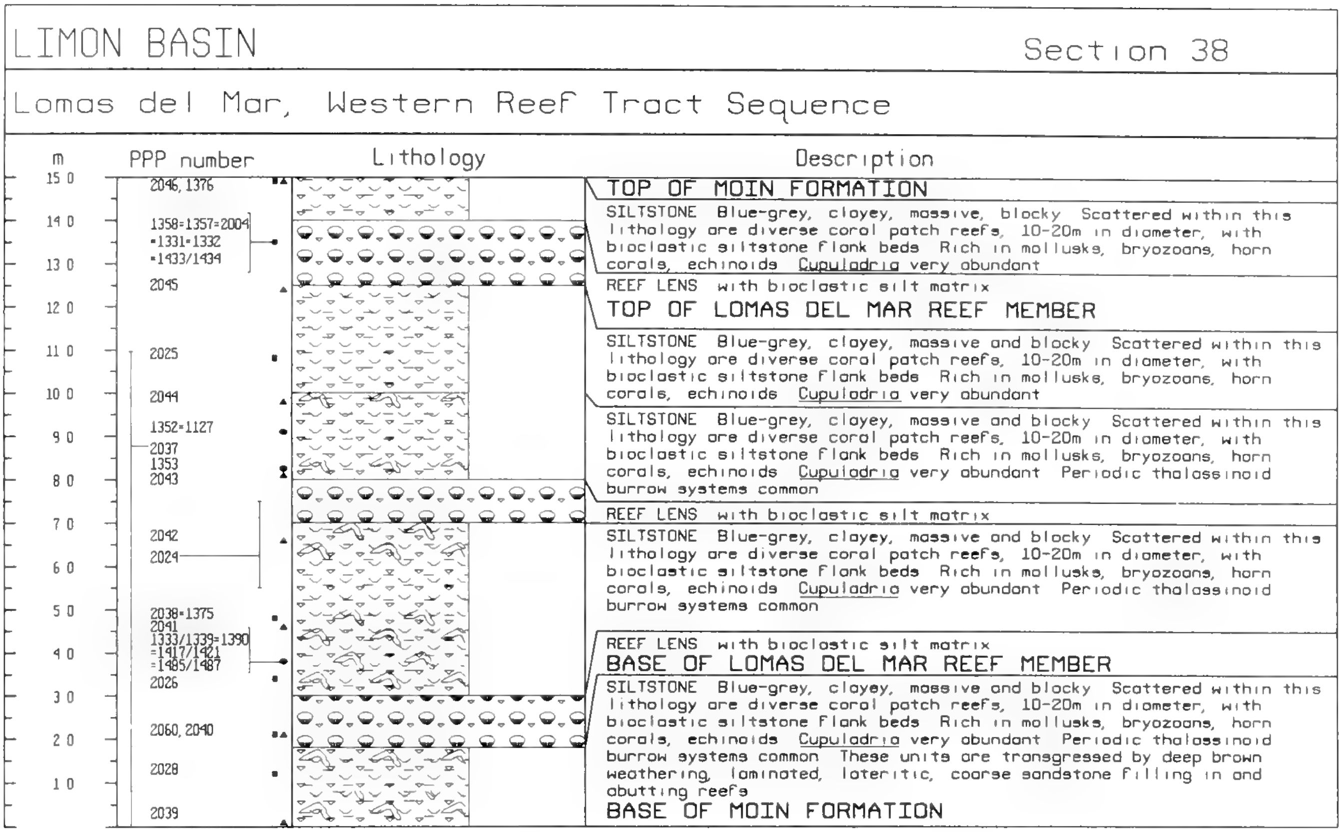
SILTY SANDSTONE Blocky, shelly, calcarenitic, volcaniclastic, with clayey matrix Rich in micromollusks and visible foraminifera

SILTY MUDSTONE Grey to greenish-blue Rich in visible foraminifera

SANDSTONE Blue-grey, clayey, volcanic, with scattered basalt grains (2mm) Packed with micromollusks The upper surface has arthropod burrows

SILTY CLAYSTONE Massive, grey-green-blue, with occasional scaphopods

BASE OF MOIN FORMATION



TOP OF MOIN FORMATION

SILTSTONE Blue-grey, clayey, massive, blocky Scattered within this lithology are diverse coral patch reefs, 10-20m in diameter, with bioclastic siltstone flank beds Rich in mollusks, bryozoans, horn corals, echinoids *Cupuladria* very abundant

REEF LENS with bioclastic silt matrix

TOP OF LOMAS DEL MAR REEF MEMBER

SILTSTONE Blue-grey, clayey, massive and blocky Scattered within this lithology are diverse coral patch reefs, 10-20m in diameter, with bioclastic siltstone flank beds Rich in mollusks, bryozoans, horn corals, echinoids *Cupuladria* very abundant

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BASE OF LOMAS DEL MAR REEF MEMBER

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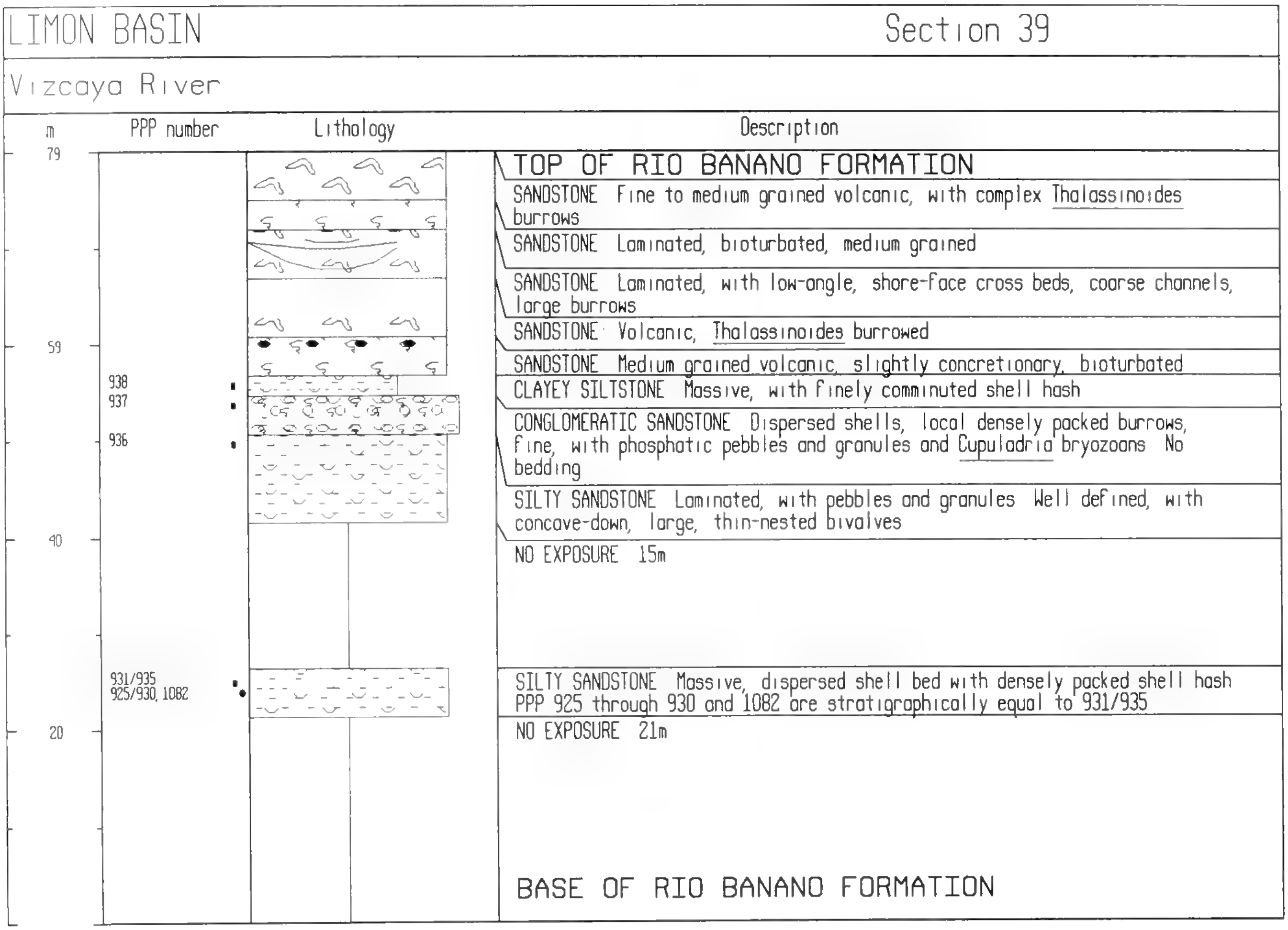
BASE OF MOIN FORMATION



LIMON BASIN

Section 39

Vizcaya River

TOP OF RIO BANANO FORMATION

SANDSTONE Fine to medium grained volcanic, with complex *Thalassinoides* burrows

SANDSTONE Laminated, bioturbated, medium grained

SANDSTONE Laminated, with low-angle, shore-face cross beds, coarse channels, large burrows

SANDSTONE Volcanic, *Thalassinoides* burrowed

SANDSTONE Medium grained volcanic, slightly concretionary, bioturbated

CLAYEY SILTSTONE Massive, with finely comminuted shell hash

CONGLOMERATIC SANDSTONE Dispersed shells, local densely packed burrows, fine, with phosphatic pebbles and granules and *Cupuladria* bryozoans No bedding

SILTY SANDSTONE Laminated, with pebbles and granules Well defined, with concave-down, large, thin-nested bivalves

NO EXPOSURE 15m

SILTY SANDSTONE Massive, dispersed shell bed with densely packed shell hash PPP 925 through 930 and 1082 are stratigraphically equal to 931/935

NO EXPOSURE 21m

BASE OF RIO BANANO FORMATION

# INDEX