Caribbean Journal of Science, Vol. 41, No. 3, 374-391, 2005

An Introduction to the Geology of the Bocas del Toro Archipelago, Panama

A. G. Coates[1], D. F. McNeill[2], M-P. Aubry[3], W. A. Berggren[4], L. S. Collins[5]

[1]*Smithsonian Tropical Research Institute, Apartado 2072, Republic of Panama*
[2]*Division of Marine Geology and Geophysics, Rosensteil School of Marine and Atmospheric Science, University of Miami, Florida, 33149, USA*
[3]*Department of Geological Sciences, Rutgers University, Wright Labs, 610 Taylor Road, Piscataway, New Jersey, 08854-8066*
[4]*Woods Hole Oceanographic Institute, Department of Geology and Geophysics, Woods Hole, Massachusetts, 02543, USA and Department of Geological Sciences, Rutgers University, Wright Labs, 610 Taylor Road, Piscataway, New Jersey, 08854-8066, USA*
[5]*Department of Earth Sciences, Florida International University, Miami, Florida, 33199, USA*
Corresponding author: coatesj@hardynet.com

ABSTRACT.—We review the stratigraphy of the Neogene rocks of the Bocas del Toro archipelago, western Caribbean coast of Panama, and provide new geological maps and a preliminary description of new Neogene formations on the islands of Bastimentos and Colon. The Punta Alegre and Valiente formations range in age from 19 to 12 Ma. After a hiatus from 12 to 8 Ma, a transgressive/regressive sedimentary cycle is recorded by the Tobobe, Nancy Point, Shark Hole, Cayo Agua, and Escudo de Veraguas formations (=the Bocas del Toro Group), that range in age from 7.2-5.3 to 1.8 Ma. In contrast, in the northern region, the Old Bank, La Gruta, and Ground Creek units and the Swan Cay Formation only range in age from about 3.5 to 0.78 Ma. The hiatus represented by the unconformity is from 12 to 3.5 Ma. We integrate the geology of the Bocas del Toro archipelago into a brief history of the Neogene of the lower Central American isthmus.

KEYWORDS.—Neogene, Bocas del Toro, Central American Isthmus

INTRODUCTION

Background

This overview paper provides an introduction to the geological foundation of the modern biological systems found today in the Bocas del Toro region. The study of the geology of Bocas del Toro was undertaken as part of the Panama Paleontology Project (PPP; Collins and Coates 1999), a collaborative research program to study sediments deposited during the last 20 million years (involving the Miocene, Pliocene, and Pleistocene Epochs, which are together known as the Neogene) along both sides of the isthmus of Central America and of northern South America (Fig. 1).

We systematically mapped the whole region, named the physical stratigraphic formations (Fig. 2) and located the rich and diverse macrofossil sites. After additional paleomagnetic studies and radiometric dating, these studies provide a detailed geologic history of the region and a temporal framework for the evolutionary and ecological studies of the macrobiota.

Regional Geologic History

The Central American isthmus forms the western margin of the Caribbean Plate 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 (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 (now confounded by compression from the west-northwestward-moving South American Plate). In the east, it is bounded by the Lesser Antilles subduction zone. The western margin of the Caribbean Plate is more complex; in the northern part, the Cocos Plate is in contact with the Caribbean Plate.

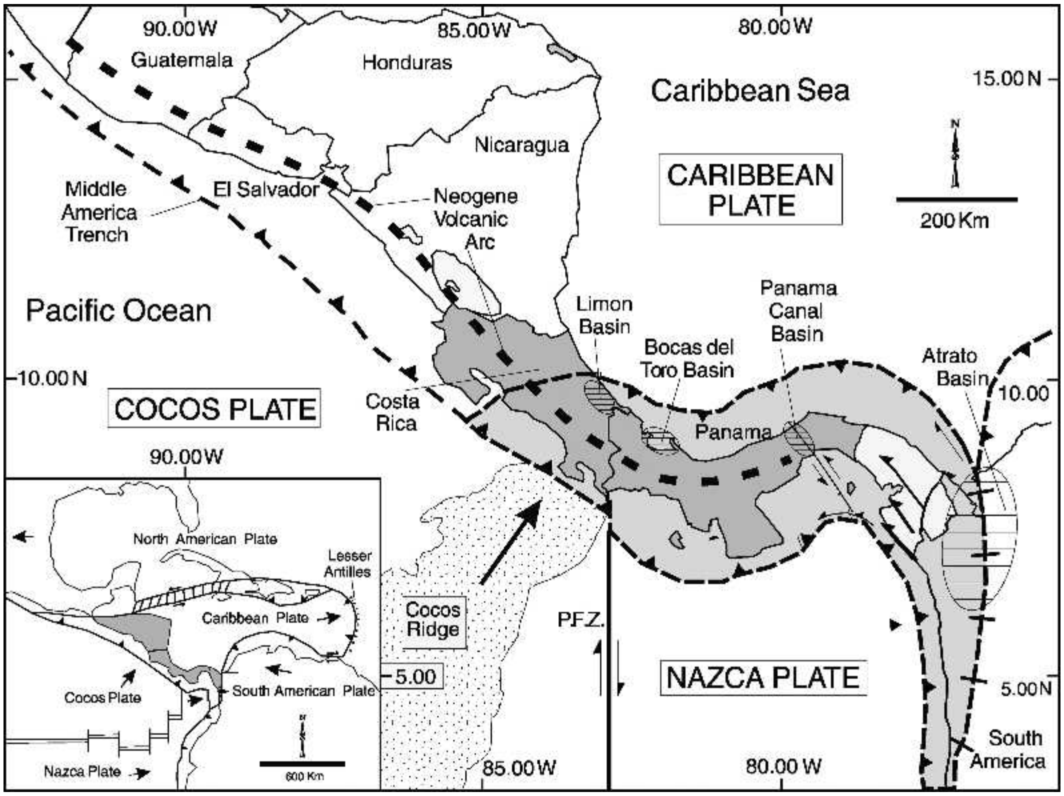


FIG. 1. Map of southern Central America (dark shading) and the Panama microplate (pale shading). Dashed lines with teeth mark zones of convergence; zippered line is Panama-Colombia suture. Very heavy dashed line marks location of Neogene volcanic arc. Fine arrows are Paleogene faults; thick arrows are late Neogene faults. Principal Neogene sedimentary basins located by striped ovals. Spotted pattern defines the Cocos Ridge. Arrows on the inset indicate directions of relative motions of the plates. PFZ = Panama Fracture Zone

In the southern portion of the western margin, a triple junction brings the Cocos and Nazca Plates in contact with the small Panama Microplate (Fig. 1). The Panama Microplate appears to have formed by northward escape from compression of the South American and Cocos/Nazca plates (Burke and Sengor 1986; Coates et al. 2004). Much of Central America lies either on the trailing western edge of the Caribbean Plate or on the Panama Microplate but a portion also lies on the southwestern corner of the North American Plate (Fig. 1).

Since their formation in the Miocene, the Nazca and Cocos plates have impinged on Central America with different motions. The Cocos Plate (Fig. 1), with relative northeasterly motion, is subducting vigorously under northern Central America as far south as the Costa Rica-Panama border and is associated with active seismicity and volcanism. Northern Central America also has a broad zone of older continental crust, and has a geologic history extending back to the early Paleozoic (Donnelly et al. 1990). In contrast the Nazca Plate has a relative easterly motion but is not actively subducting under Panama. The Panama Microplate is formed of oceanic crust that is typical of the widespread basalt plateau that underlies much of the rest of the Caribbean Plate (Case et al. 1990).

Three major movements have affected the Neogene tectonic evolution of the southern Central American isthmus (CAI; Kolarsky et al. 1995; Coates and Obando 1996). The first is convergent tectonics of the eastern Pacific subduction zone (Fig. 1), the primary driving force that created the Central American isthmus by forming a

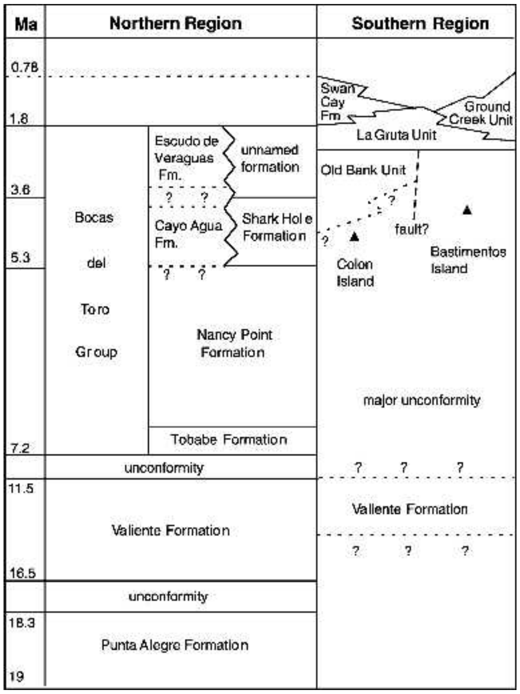


FIG. 2. Physical stratigraphic nomenclature of the Northern and Southern regions of the Bocas del Toro archipelago with ages in millions of years

volcanic arc extending southwards from North America. It forms part of an extensive zone of subduction that runs the length of the western margin of North, Central, and South America (Astorga et al. 1991).

The second tectonic effect was subduction of the Cocos Ridge (Kolarsky et al. 1995; Collins et al. 1995), a lighter and relatively thick welt of Pacific oceanic crust, under the Central American volcanic arc in Costa Rica (Fig. 1). This hard-to-subduct ridge rapidly elevated the Central American Isthmus from the Arenal volcano in Costa Rica to El Valle in Panama (de Boer et al. 1988) culminating in the center where the Talamanca Range rises to about 4000 m. The elevation of the Talamanca range probably substantially reduced the number of marine connections between the Pacific and Caribbean.

The third tectonic influence on southern Central America was the collision of the Central American volcanic arc (the western margin of the Caribbean plate) with northwestern South America (Coates et al. 2004; Silver et al. 1990; Mann and Kolarsky 1995). The relative northwestward movement of South America (Fig. 1) has increasingly compressed the southern Caribbean Plate margin in the late Neogene. This convergence has uplifted eastern Panama and the northern Andes of Colombia and Venezuela.

The resulting shoaling of the CAI (detected paleoceanographically by a marked divergence between planktonic foraminiferal oxygen isotope records (a proxy for salinity changes) was to less than 100 m from 4.7-4.2 Ma (Keigwin 1982; Haug and Tiedemann 1998; Gussone et al. 2004). This initiated the development of the modern Atlantic-Pacific contrast in sea surface salinities (SSS), with higher SSS in the Caribbean.

Recent studies by Tiedemann, Steph, and Groenveld and others (Poster sessions, American Geophysical Union Meeting, 2004 and pers. comm. 2005) have suggested 2.8 as the time of final closure of the CAI. Using Ca/Mg measurements of planktonic foraminifera, they show that Caribbean and Pacific Sea Surface Temperature (SST) records are similar from 5-2.8 Ma. Then larger scale sea level fluctuations with 41 kyr. cyclicity became dominant in response toamplification of the Northern Hemisphere glaciation. After 2.8 Ma, glacial stages, when sea level is lowest, show minimum Pacific SSTs, but maximum SSTs occur in the Caribbean. This anomaly is explained by low sea stands preventing cooler less saline water from entering the Caribbean from the Pacific (the CAI is emergent), and the reverse applies in interglacials when sea level is high, breaching the CAI.

The closure of the Isthmus of Panama triggered profound environmental changes on land and in the sea. The formation of a bridge between the North and South American continents gave rise to the Great American Biotic Interchange on land (Webb and Rancy 1996; Webb 1999). Less well known are the timing and nature of the changes in the sea, consequent upon the growth of the Central American volcanic arc and its eventual collision with South America. This created a marine barrier that increasingly affected ocean circulation during Neogene time. In the process, a striking contrast evolved between the relatively warm, more saline, nutrient-poor Caribbean and the more seasonal, less saline and more pelagically productive eastern Pacific (Jackson and D'Croz 1999). These environmental changes apparently altered the course of evolution, first of the deep-water planktonic organisms like radiolaria and diatoms from about 15 Ma, and then successively shallower taxa until complete emergence at about 2.8 Ma. By this time, the eastern Pacific had evolved rich pelagic biotas but poorly developed, low diversity, coral reefs (Jackson and D'Croz 1999). In contrast, the Caribbean had become dominated by coral reef-seagrass-mangrove coastal ecosystems (Collins et al. 1996) and a profound taxonomic turnover had occurred in corals and mollusks (Budd and Johnson 1997, 1999; Jackson et al. 1993).

Much of this history is documented in the long geological section preserved around the Bocas del Toro Archipelago whose deposits range in age from the early Miocene (about 20 Ma). The sequence can be assigned to four phases in the rise of the isthmus as follows: 1) Deposition of lower bathyal, pre-isthmian, oceanic sediments in early Miocene time (21.5-18.5 Ma); 2) Growth of a volcanic arc during middle Miocene time (~18 to ~12 Ma) characterized by terrestrial and marine deposits including columnar basalt and flow breccia, coarse volcanic sediments, and scattered small coral reefs; 3) Extinction of the arc about 12 Ma and subsequent extensive emergence and erosion; and 4) Subsidence of the volcanic arc during the latest part of Miocene time (~7.2-5.3 Ma), resulting in a marine transgression, followed by a marine regression, that culminated in the widespread development of Plio—Pleistocene reefs (McNeill et al. 2000; Coates et al. 2003).

STRATIGRAPHY

For the purposes of this paper, we first describe the stratigraphic units that occur in the south and north of the Bocas del Toro Archipelago. These are discussed separately because the sequences are different in these two areas (Fig. 2). We then attempt to synthesize the geologic history of Bocas del Toro and compare it with adjacent regions in Costa Rica, Darien, Panama, and the Atrato Valley, Colombia.

1) The northern region comprises Swan Cay, Colon, Pastora, San Cristobal, Carinero, and Bastimentos islands, and the Zapatillo Cays.
2) The Southern region comprises the islands of Popa, Deer, Cayo Agua, and Escudo de Veraguas, and the Valiente Peninsula.

In general, the northern region exhibits a late Pliocene-Pleistocene succession of shallow water sediments, especially coral reef deposits, that either unconformably overlie middle Miocene volcanic arc basalt (Bastimentos Island) or rest on a thick (>2500 m) siliciclastic shale (Colon Island) that is late Pliocene at its top and of unknown age at its base. This suggests that there is a major structural break in the volcanic arc basement rocks between Bastimentos and Colon islands. The southern region reveals a more extensive volcanic arc suite of lower and middle Miocene rocks, including a sequence of deep-sea ooze, basalt, coarse volcanic sediments and small scale patch reefs, that tracks the onset and rise of an active volcanic arc in the Bocas del Toro region. Subequently, an unconformably overlying, non-reefal, upper Miocene and Pliocene, marine, transgressive/regressive shelf sequence was deposited.

Stratigraphic definitions

Stratigraphy of sedimentary rocks involves the integration of four main kinds of units, each of which provides the basis of a subdiscipline of stratigraphy. The first, lithostratigraphy, describes the physical stratigraphic units and their three-dimensional geometry across the region studied. Each mappable unit or *Formation* is distinguished by its rock type or lithology and is named, usually from the place where it most typically can be observed. A series of formations deposited in vertical succession in a genetically related depositional episode may be lumped together as a *Group*.

If the contact of two lithostratigraphic units shows evidence of a break in sedimentation this line is called an *unconformity*. Unconformities usually reflect major geological events (like tectonic uplift or sea level change) in the area where they occur. The significance of unconformities will vary depending on how different the units are above and below, and how much time the break represents. From the nature of the different sediments and their associated sedimentary structures and fossils, the physical environment and water depth in which the formation was deposited can be reconstructed. Fig. 2 outlines the nomenclature of the lithostratigraphy of the Neogene formations of the Bocas del Toro archipelago.

The second subdiscipline is biostratigraphy, which takes advantage of the fossil content of rocks, and is based on the *range* of species, i.e., the stratigraphic interval between two specific stratigraphic horizons corresponding to the lowest (LO) and the highest (HO) occurrence of a taxon. The basic unit of biostratigraphy is the *biozone*, a stratigraphic interval defined between LO and HO of taxa selected for their distinct morphology and vast geographic distribution. Biozones allow *stratigraphic correlation*, the fundamental procedure of establishing that two horizons have the same relative age. Chronostratigraphy, the third element of stratigraphy, is a system of reference for the relative dating of sediments. Its basic unit is the *stage*, defined by its base (= a stratigraphic horizon) and a stratotype (a stratigraphic interval). Correlation of rocks in a given basin to a stage is established via biostratigraphy. Stages are grouped in a nested hierarchy of *Series, Systems, and Erathems.* Their temporal equivalents are called *Ages, Epochs, Periods, and Eras,* respectively.

The fourth subdivision, geochronology, is the science of numerical time. Whereas chronostratigraphy deals with relative time (younger/older), geochronology transforms specific stratigraphic horizons into numerical markers. Geochronology uses radioisotopic ages and/or astrocyclicity (i.e., Milankovich periodicity), usually in conjunction with paleomagnetic stratigraphy, to determine the ages of chronostratigraphic and biostratigraphic boundaries. i.e. the stratigraphic level common to two successive stages or biozones. Numerical ages vary depending on the criteria selected in the building of a gechronologic framework or *time scale.* The ages given below refer to the time scale of Berggren et al. (1995). The boundaries between lithostratigraphic units may be of the same age regionally, but over larger regions they may become younger or older in age as the physical environments they represent migrated across the sedimentary basin through time. They are then said to be *diachronous.*

The southern region

Each lithostratigraphic unit, starting with the lowest, will first be named and described, and then evidence for its age and environment of deposition will be added. For a more detailed description of the stratigraphy of these units see Coates et al. (1992, 2003) and Coates (1999).

Punta Alegre Formation.—This formation is named for Punta Alegre, the nearest small village to its solitary exposure. Punta Alegre is located on the western tip of the north coast of Bahia Azul (Bluefield Bay) in the northern part of the Valiente Peninsula (Fig. 3). The formation can be observed in a prominent small cliff about 1.3 km northwest of the village, on the west-facing coast 1 km south of Valiente Point. It consists of clay and silty ooze containing abundant calcareous nannofossils and benthic and planktonic foraminifera (see Coates et al. 2003, Tables 1, 2), many of the latter are easily seen by a hand lens and by the naked eye. The formation can be seen to lie underneath weathered coarse volcanic flow breccia (the broken up bouldery rock that is crated when lava flows and cools at the same time). From its abundant planktonic foraminifera and calcareous nannofossils, the age of the Punta Alegre Formation is 19-18.3 Ma. (Coates et al. 2003), and by its benthic foraminifera it is interpreted to have been deposited in water depths of 100—2000 m (Coates et al. 2003).

The Valiente Formation.—This unit overlies the Punta Alegre Formation and crops out extensively on the Valiente Peninsula (Fig. 3) and nearby Deer and Popa islands (Fig. 4). The Valiente Formation is of complex and highly variable lithology because it represents the suite of facies, marine and terrestrial, igneous and sedimentary, that is associated with an active emergent volcanic island arc. It includes columnar basalt, basalt flow breccia, pyroclastic tuff (airborne volcanic ash deposits), fluviatile/estuarine conglomerate, marine debris flows and coral reef lenses. The latter consist of several species of *Montastraea* (including *M. imperatoris* and *M. canalis*), massive *Porites waylandi* and thin branching *Stylophora* (possibly *S. granulate*; Ann Budd pers. comm. 2005). These facies intercalate and replace each other over very short distances, both laterally and vertically (for detailed descriptions of the facies, see Coates et al. 2003). Fig. 3 shows that the basalt lava and flow breccia facies form a core around which the other facies are distributed peripherally as terrestrial, coastal or marine slope deposits. Planktonic microbiotas and radiometrically dated basalt in the se-

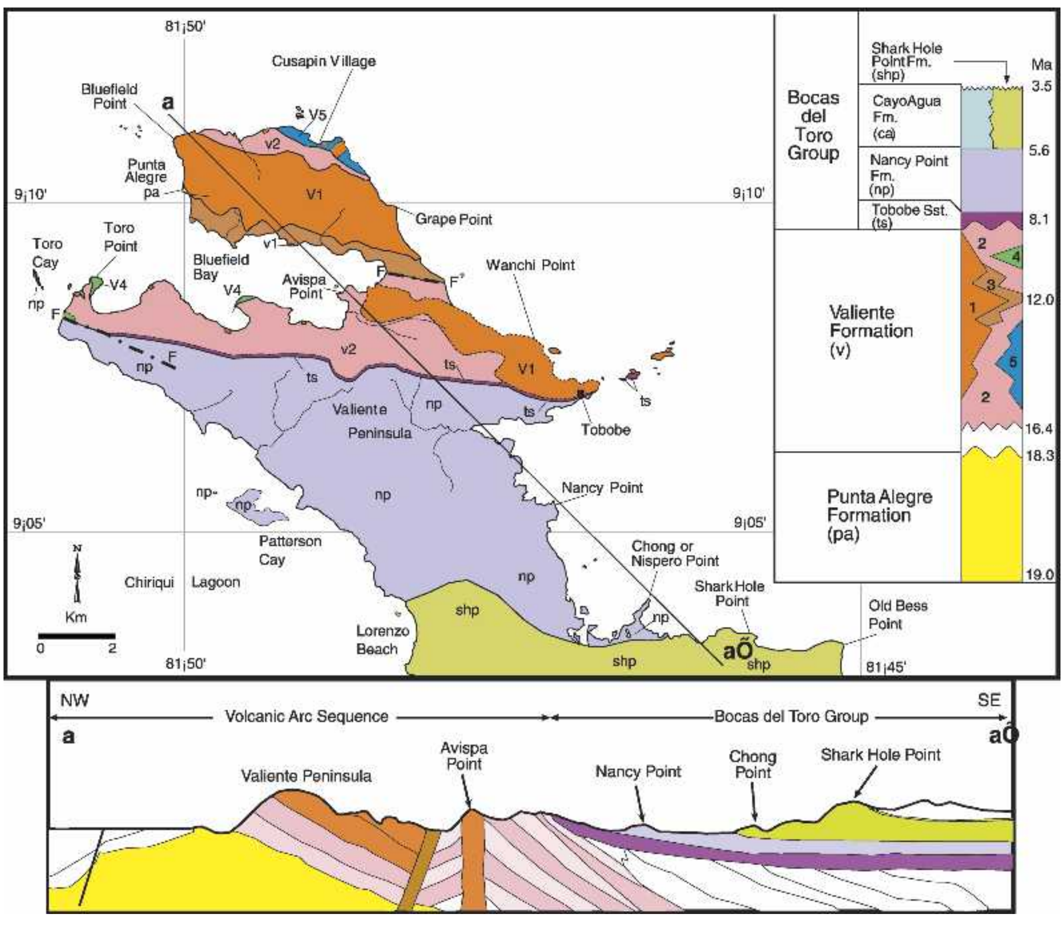


FIG. 3. Geological map and cross section (a – á) of the Valiente Peninsula, Bocas del Toro, western Panama, showing the distribution of the Punta Alegre and Valiente formations and the Bocas del Toro Group. The five lithofacies of the Valiente Formation are indicated by separate colors and numbers on the key (upper right) as follows; v1) basalt lava and flow breccia facies; v2) coarse volcaniclastic facies; v3) pyroclastic facies; v4) coral reef facies; v5) marine debris flow and turbidite facies.

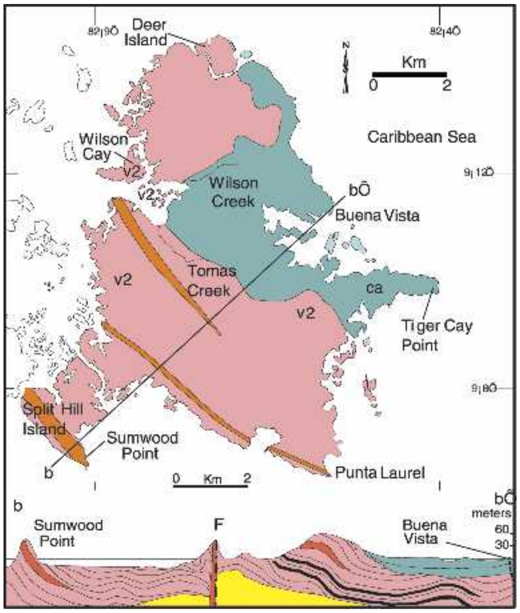


FIG. 4. Geological map of Popa Island. Section (b-b′) shows the Valiente Formation on Popa Island, where it is unconformably overlain by the Pliocene Cayo Agua Formation (ca). Numbers and symbols as for Figure 3. On Popa Island, only the v1 basalt flow facies and the v2 coarse volcaniclastic facies (not associated with reef lenses) are present, with thin layers of low rank coal, an example of which is exposed along the coast immediately north of Punta Laurel. A prominent basalt dike is exposed at the tip of the Punta Laurel (here shown in red as v1 facies) where it cuts the Valiente Formation.

quence indicate that the Valiente Formation ranges in age from 16.5-11.5 million years old and includes marine deposits from near-shore to as deep as 1000 m, as well as several types of terrestrial deposits (Coates et al. 2003).

Bocas del Toro Group.—Columnar basalt and pyroclastic and fluviatile rocks of the Valiente Formation required extensive emergence of parts of the growing volcanic arc (columnar basalt is formed by the cooling of lava ponded lakes). About 12 Ma, the arc had become inactive and recent studies in Darien, Panama (Coates et al. 2004), suggest that the collision of the southern tip of the Central American volcanic arc with South America was initiated at the same time. These events may explain the major unconformity in the Bocas del Toro Archipelago above the Valiente Formation, signifying extensive emergence and erosion of the volcanic arc from ~11.5-~7.2 Ma (Fig. 2, 3). This unconformity can be clearly observed in the inner islands of the Plantain Cays and along the coast immediately to the west. The underlying columnar basalt of the Valiente Formation can be seen on the north side of the Cays and the fossiliferous conglomerate and sandstone of the Tobobe Sandstone on the south side.

The Bocas del Toro Group signifies a new depositional cycle as a marine transgression submerged the older eroded volcanic arc rocks. The oldest sediments thus represent the first shallow-water, beach, and near-shore sand deposits. As the transgression developed, subsequent overlying marine units reflect deeper water deposition until the reverse occurred and the sea regressed to shallow water again. Thus, the units of the Bocas del Toro Group are genetically related and document a single marine transgressive/regressive event. The most continuous section lies along the east and west coasts of the Valiente Peninsula (Fig. 3) where it ranges in age from late Miocene (Messinian, 7.2-5.3 Ma) to late Pliocene (~3.5 Ma).

Tobobe Sandstone.—This lowest unit is a pebble conglomerate that passes up into clean, hard quartz sandstone containing sand dollars, spatangoid echinoids, mollusks, including the large, thin-shelled bivalve *Amusium*, vermetids and serpulids, as well as an array of infaunal burrow structures. It is best observed on the small Plantain Cay and an adjacent smaller unnamed island to the west (Fig. 3). The deposit represents a beach and near-shore sand body and documents the earliest stage of the marine transgression. Planktonic foraminifera from laterally equivalent deposits on Toro Cay (Fig. 3) indicate that the age of the unit is Messinian (7.2-5.3 Ma). Here the deposit contains a variety of mollusks including turritellids and pectens, erect bryozoa, and echinoids. Classic examples of complex thalassinoid burrow systems constructed by callianasid crustaceans are also present.

Nancy Point Formation.—It was named for the promontory called Nancy Point which lies 2.5 km southwest of the village of Tobobe (Fig. 3). The formation is almost continuously exposed southward along the coast as far as Chong Point (= Nispero Point). The Nancy Point Formation is conformable with the Tobobe Formation below and the Shark Hole Point Formation above (Fig. 2 and 3). It consists of shelly, muddy and silty sandstone, and muddy siltstone with occasional coarse volcaniclastic and bioclastic sandstone beds. It contains scattered mollusks and occasional leaves and plant fragments with diverse moderately abundant molluscan assemblages throughout the section and several, rich, low-diversity, thick-shelled mollusk beds at the base.

The transition from Tobobe Sandstone to Nancy Point Formation is best seen on Toro Cay (Fig. 3) where dark blue-gray, silty sandstone, typical of the Nancy Point Formation, contains occasional, clearly defined infaunal burrow systems and extremely abundant and diverse mollusks. It overlies coarse, channeled Tobobe Sandstone with only a 10-m exposure gap. Nancy Point Formation benthic foraminifera indicate that deposition of the Nancy Point Formation was in 200-500 m. water depth (Collins 1993) demonstrating that relatively rapid deepening took place from near-shore (Tobobe Sandstone) to upper slope (Nancy Point Formation). This represents the maximum depth of the transgressive/regressive cycle. Planktonic foraminifera and calcareous nannofossils date the Nancy Point Formation as Messinian (7.2-5.3 Ma), the same time range as for the Tobobe Sandstone. Within that time frame the Nancy Point Formation is younger because it overlies the Tobobe Sandstone.

Shark Hole Point Formation.—It is named for the promontory of the same name that lies 3 km east of Chong Point (Fig. 3) and the stratotype lies along the coast between Chong Point and Bruno Bluff, south of Old Bess Point. The Shark Hole Point Formation conformably overlies the Nancy Point Formation (Fig. 2 and 3) 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. The Shark Hole Formation 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. Benthic foraminifera indicate that the paleobathymetry of this unit ranges from 100-200 m (Collins 1993). This represents the first stage of the regressive phase of the Bocas del Toro Group transgressive/regressive cycle. Calcareous nannofossils and planktonic foraminifera are abundant in several horizons and suggest the age of the formation is early Pliocene (5.3-3.6 Ma).

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 through stratigraphic correlation.

The Escudo de Veraguas Formation is known only from the island of the same name that lies 27 km east of Nancy Point (Fig. 5) . Its stratotype, for the lower part of the formation, is along the coast on the east side of the V-shaped embayment situated in the central part of the north coast, about 1 km east of Long Bay Point (Fig. 5). The stratotype for the upper part of the formation lies along the west coast for about one km south of Long Bay Point.

Lithologically, the Escudo Formation consists of, in the upper part (1.8 Ma), pervasively bioturbated clayey siltstone and silty claystone, with frequent concretions, and scattered shelly hash, often with scattered whole and diverse mollusks, small, cornute, ahermatypic corals. The lower part of the formation (3.5 Ma) is more indurated with very common and densely packed cemented burrow concretions and thalassinoid galleries at the base, scattered ahermatypic corals through the middle part, as well as variably abundant mollusks, and at the top a coral biostrome dominated by *Stylophora* and sand dollars. The top and botton units suggest deposition in inner

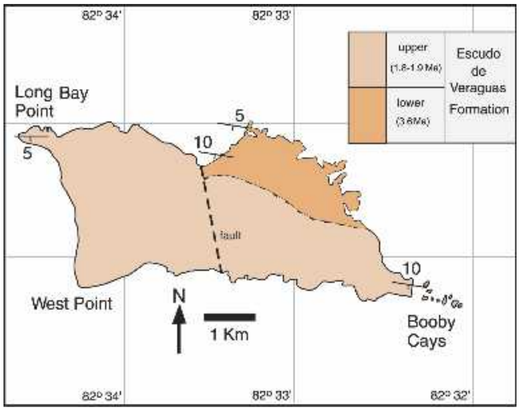


FIG. 5. Geological map of Escudo de Veraguas island. Ages in millions of years in brackets for lower and upper parts of the Escudo de Veraguas Formation.

neritic water depths, but the middle part of this lower succession has abundant benthic foraminifera indicating deposition in outer neritic to upper bathyal water depths (Collins 1993).

Cayo Agua Formation.—This formation was named for the island that lies about 6 km to the west of Toro Point, Valiente Peninsula. The formation is well exposed along the east coast (Fig. 6) and consists lithologically of pervasively bioturbated, muddy, silty 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 Formation is consistently coarser-grained, with common basalt grains and granules, phosphatic pebbles, and wood fragments. A distinctive marker bed of corals occurs near the top of the formation and is well exposed at Tiburon Point and the unnamed point to the south. The corals appear to be mostly free living, hermatypic, grass flat corals, such as *Placocyathus* and *Manicina* (= *Teleiophyllia*), as well as ahermatypic species, and they suggest deposition in water depths of 30-50 m (Ann Budd, pers. comm. 2005). Evidence from benthic foraminifera (Collins 1993) indicates paleobathymetry of 20-80 m, overlapping the inference from lithology and coral fauna that the Cayo Agua Formation represents a shallow-water facies.

The age of the Cayo Agua Formation is dated at the base ~5.0-3.5 Ma and at the top 3.7-3.4 Ma, which suggests it is a contemporary, shallow water equivalent of the Shark Hole Point Formation and the lowermost part of the Escudo de Veraguas Formation.

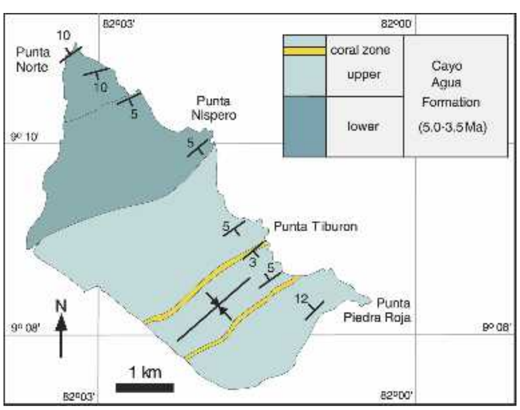


FIG. 6. Geological map of Cayo Agua. Ages in millions of years.

The northern region

The islands in the northern region of the Bocas del Toro archipelago have a different geologic history than the southern region. Volcanic arc columnar basalts of the Valiente Formation form the basement that underlies the marine late Neogene succession, as in the southern region. While no radiometric dates for these basalts are available, we can presume they are part of the same volcanic arc that went extinct and cooled after the middle Miocene (~12 Ma). In all the Northern Region, the sediments unconformably overlying the Valiente Formation basalt are Plio-Pleistocene in age. The upper Miocene succession of Tobobe Sandstone, Nancy Point, and Shark Hole formations are absent. Furthermore, the northern units are characterized by a major component of coral reef limestone.

The geology of Colon and Bastimentos islands are currently being studied and the formal designation of the lithostratigraphic units and their ages is not yet finalized. In general, the sequence is younger than the section to the south with the exception of the Escudo de Veraguas Formation. The oldest units on Colon and Bastimentos islands may overlap in time with the top of the Cayo Agua and Shark Hole Point sequences at ~3.5 Ma.

Valiente Formation.—The spectacular exposures along the northwestern coast of Bastimentos Island (Fig. 7) of columnar basalt and flow breccia are assigned to the Valiente Formation solely on their great similarity in lithology. The exposures range from Toro Point to the eastern side of

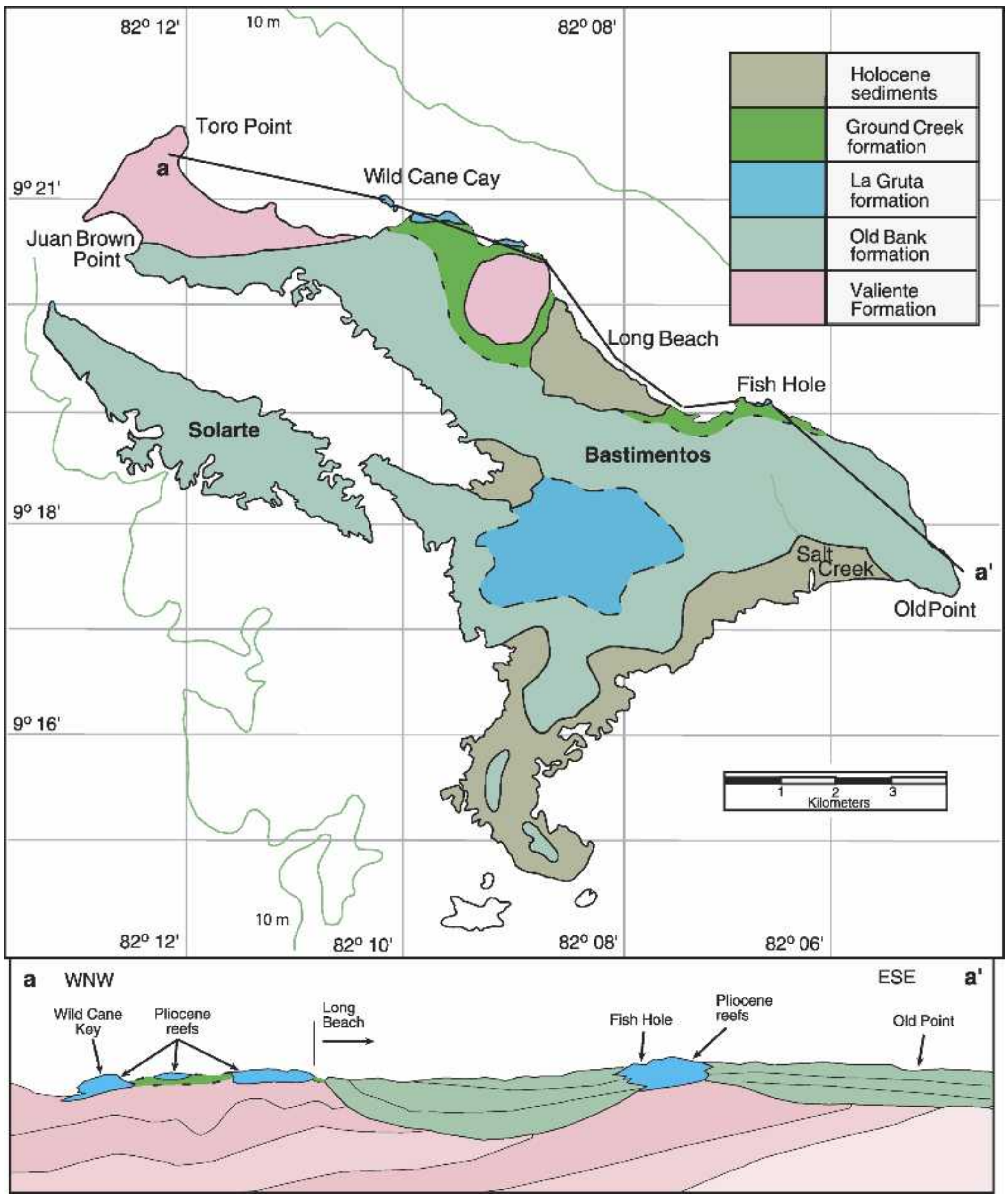


FIG. 7. Geologic map and section (a-a′) of Bastimentos

Dreffe Beach and occur also at the western end of Long Beach. These basalt units probably form the basement of the entire Bocas del Toro Archipelago.

Unnamed Formations of Colon and Bastimentos islands.—There are three major lithostratigraphic units (Fig. 2).

Old Bank Unit (informal field name).—This is the oldest unit, and it crops out extensively in the southern half of Colon Island (Fig. 8) where it is crossed by the Bocas del Drago road along which there are several good exposures. It also occurs in the northeast of the island where it forms a distinct escarpment parallel to the coast. Many streams have waterfalls where they cross this scarp with good exposures. The same unit crops out on Bastimentos Island (Fig. 7). There are exposures from Juan Brown Point eastwards along, and inland of the south coast, in steep stream courses flowing down from the ridge formed by its outcrop, which parallels the coast.

On Colon Island the Old Bank Unit consists mostly of a blue-grey mudstone with occasional thin sandstone stringers, fine volcanic conglomerate and volcanic boulder beds. On Bastimentos, it may be micaceous and sandier, with wood fragments and sparse mollusks including turritellids and *Anadara*. Preliminary field observations suggest it is an inner shelf deposit flanking volcanic islands and that it is about 3.5-2.0 Ma.

La Gruta Unit (informal field name).—On Colon Island (Fig. 8), an extensive recrystallized reef and reef rubble deposit is exposed in the north central part of the island. Eastward from Hill Point it forms distinctive ridge running parallel to the north coast towards Mimitimimbi Creek. The limestone extends southward as far as La Gruta, a locally famous bat cave. Around La Gruta, the limestone is a reef deposit with numerous large coral colonies but the limestone grades into fore-reef rubble northeastwards toward the mouth of Mimitimimbi Creek where it is well exposed on the coast. Both the reef and fore-reef deposits are heavily fractured to produce a rubbly rock unit when exposed. Earthquakes and uplift are likely responsible for this pervasive fracturing.

Twenty species of corals have been identified from the limestone near Hill Point, the most abundant being *Caulastraea portoricensis*, *Stylophora granulata*, *Agaricia (= Undaria agaricites), Colpophyllia natans, Montastraea faveolata,* and *Mycetophyllia danaana* (Ann Budd, pers. comm. 2005). Exposure of similar limestone also occurs immediately to the North of Paunch, on the east coast of Colon Island, and on Carinero Island (Fig. 8). At Paunch, an entirely extant fauna of corals includes *Colpophyllia natans, Diploria strigosa, Meandrina meandrites, Montastraea faveolata,* and *Agaricia (Undaria) agaricites* (Ann Budd, pers. comm. 2005).

On Bastimentos Island (Fig. 7), similar reef deposits appear to sit directly on the Miocene basalt of the Valiente Formation where they are well exposed on Wild Cane Key and along the coast for 2 km to the east. The reef limestone here is extensively recrystallized but many coral colonies can be observed. A particularly well preserved example of the La Gruta reef, packed with large and diverse coral colonies is exposed at the base of the cliffs in three small bays at Fish Hole, at the southern end of Long Beach. The most abundant species are *Dichocoenia stokesi, Manicina (Teleiophyllia) geisteri, Montastraea faveolata, M. canalis, Placocyathus variabilis, Porites waylandi, P. macdonaldi, Antillia gregorii, Goniopora imperatoris, Agaricia (Undaria) crassa*, and *Stylophora granulata*. Because >50% of this fauna is extinct, the La Gruta Formation on Bastimentos appears to be older than that on Colon Island (Ann Budd, pers. comm. 2005).

Ground Creek Unit (informal field name).—Interbedded with and overlapping onto the La Gruta Unit are back reef/reef flank deposits, dominantly shelly coral bearing bioclastic carbonate and volcaniclastic sandstone and siltstone. They are typically exposed in several stream courses in the northwest of Colon Island in a region known as Ground Creek (Fig. 8). Near Ground Creek, the unit has yielded 90 genera of bivalves and gastropods in siliciclastic mudstone and fine sandstone, where they are intercalated with thin carbonate sand containing poritid thickets and other reef patches with platy *Caulastraea portori-*

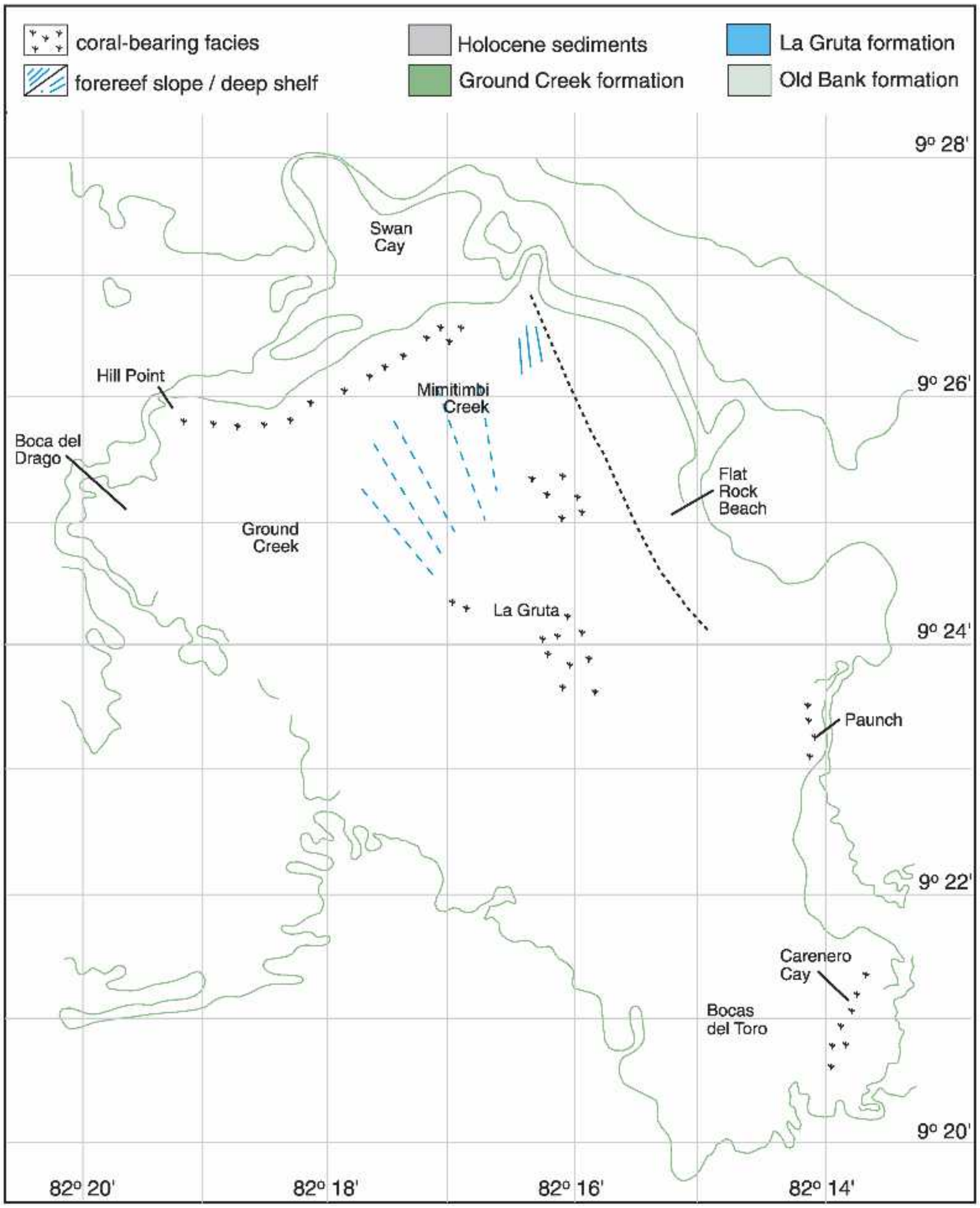


FIG. 8. Geologic map and section (a-a') of Colon Island.

censis, *Porites baracoaensis*, *Agaricia*, ?*Cladocora*, small domed ?*Favia*, *Manicina* (*Teleiophyllia*) and serpulids. Also occasionally interbedded are horizons of reworked large coral heads.

The Ground Creek unit also crops out on Bastimentos Island (Fig. 7), where it is interbedded with and overlying the La Gruta unit on Wild Cane Key, and it may also crop out around the Valiente Formation outlier at the northern end of Long Beach and overlie the reefs at Fish Hole.

Swan Cay Formation.—The formation is named for the small island of the same name that lies 1.7 km off the northern coast of Colon Island (Fig. 8). The stratotype runs from north (youngest) to south (oldest) across Swan Cay. 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 4 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 limestone. The upper 30 m includes a 4-m-thick coral bed with large *Montastraea* colonies, other corals and mollusks. The lower 30 m contains silty calcarenite with common red algae and large foraminifera, shell hash, and micromollusks. This limestone also shows evidence of frequent microfracturing, many of which are healed with secondary calcite cement. Cave deposits, about 5 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 most abundant corals are *Acropora palmata, A. cervicornis, Diploria labyrinthiformis, Montastraea faveolata, Porites furcata, Agaricia (Undaria) agaracites, Meandrina meandrites, and Dichocoenia stokesi*. Organisms from a range of depths indicate that the deposit is reworked fore-reef debris formed at about 100 m (Collins et al. 1999). Microfossils are similarly reworked. Abundant large and freshly preserved globigerinid planktonic foraminifera combined with paleomagnetic data strongly suggest that the deposit is early Pleistocene (0.78-1.77 Ma).

GEOLOGIC HISTORY

The oldest sediments recorded in the Bocas del Toro Archipelago (Fig. 9) belong to the Punta Alegre Formation and are early Miocene in age (ca. 19-18.3 Ma). They record oceanic muddy and silty ooze deposited in lower bathyal depths (1000-2000 m) and the unit is interpreted to represent the pre-isthmian Neotropical ocean. Coeval deposits, like the Uscari Formation in the southern Limón Basin (Cassell and Sen Gupta 1989; Bottazzi et al. 1994), the Clarita Formation of the Darien (Coates et al. 2004) and the Uva and Naipipi formations of the Atrato Basin (Duque Caro 1990) in northwest Colombia were also deposited at bathyal depths. Thus, prior to the collision of the southern Central American arc with South America, upper Cretaceous to lower middle Miocene rocks were deposited in abyssal to lower bathyal depths in an open-ocean, low energy, essentially non-siliciclastic sedimentary environment that was distant from South America (Coates et al. 2004).

Evidence from the overlying Valiente Formation indicates the rapid growth of a pre-isthmian volcanic arc (whose southern end was still some distance from South America) from about 16.5-12.3 Ma. During the deposition of the Valiente Formation (Coates et al. 2003), paleodepths (Fig. 9) in the region shallowed in general to upper bathyal depths (200-600 m). However, submarine topographic relief was high as volcanoes in the chain grew and coalesced, giving rise to steep sided slopes on which the sediments were deposited. Thus, near Punta Alegre in the Valiente Peninsula, and Deer Island (Coates et al. 2003) sediments were deposited in middle bathyal depths (1000-600 m) and at Avispa Point, Toro Point and Cusapin Village deposition was at upper bathyal paleodepths (600-200 m). Widespread development of columnar basalt lava, flow breccia, fluviatile to estuarine, coarse volcaniclastic deposits, lahars (terrestrial mudflow deposits), and intercalated reef lenses, packed with large coral heads, testify to the extensive emergence of the isthmian volcanic arc in the Bocas del Toro area by 12 Ma (Fig. 3).

Fig. 10 outlines paleogeographic reconstructions for these events. The volcanic arc underlying the Neogene sediments of Bocas del Toro was an active and emergent

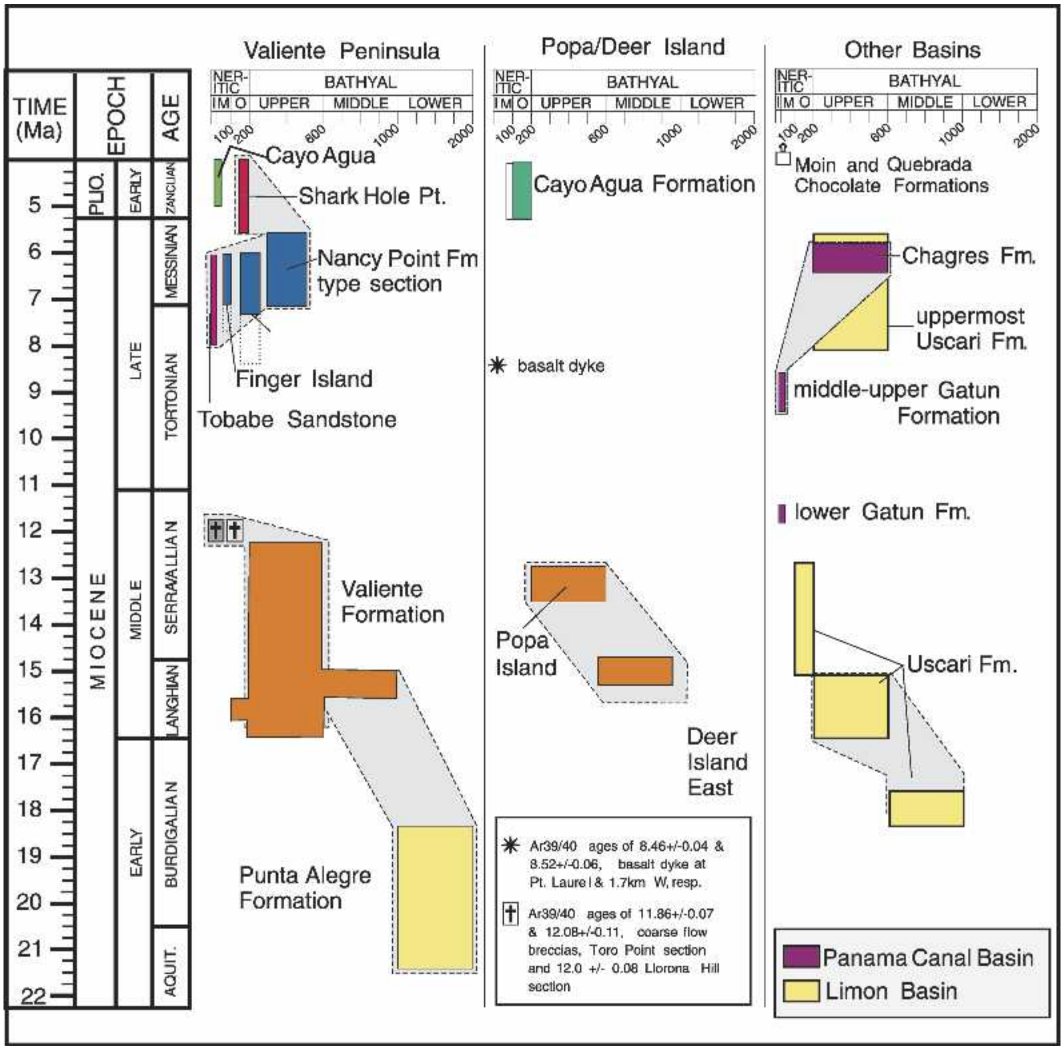
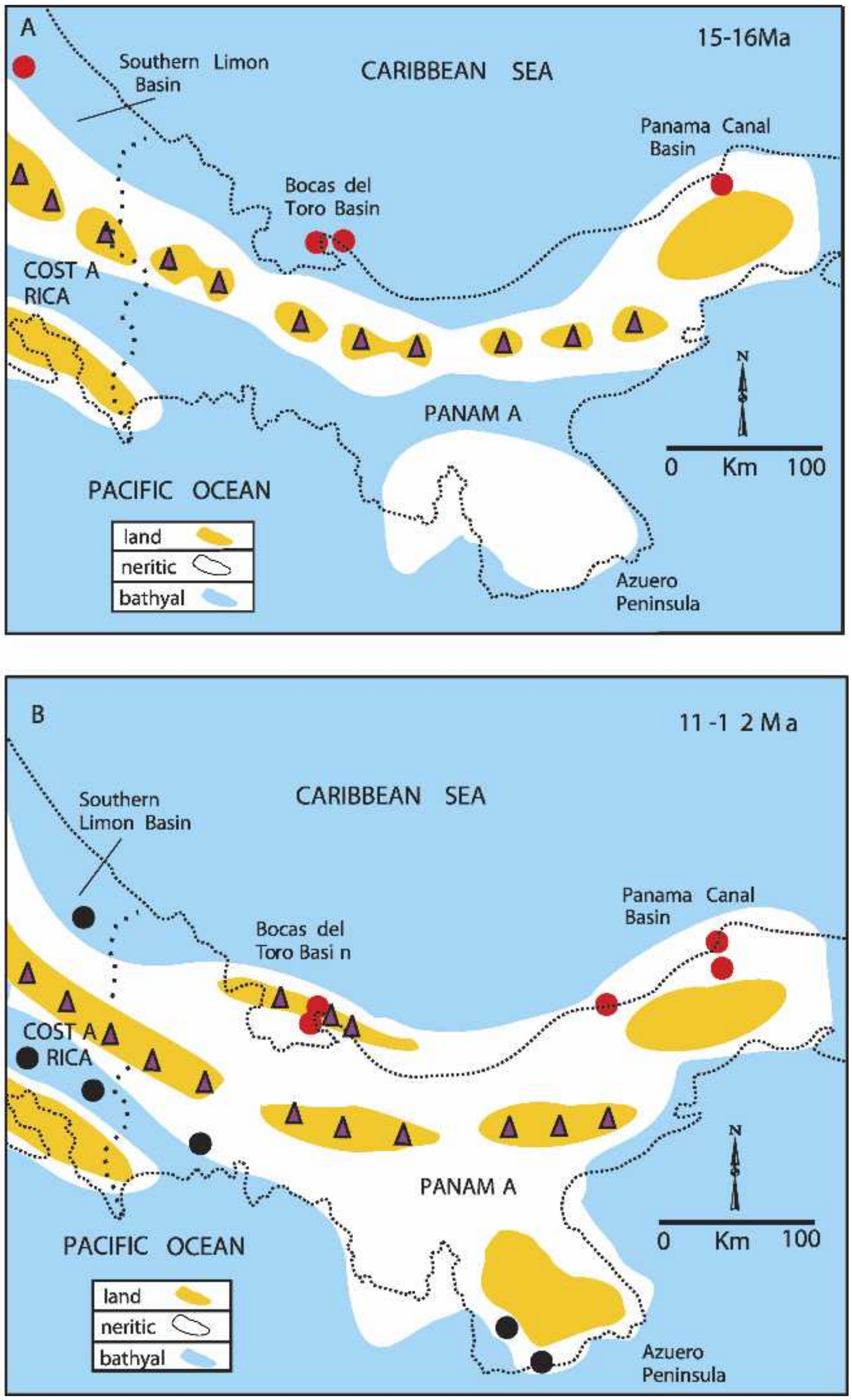


FIG. 9. Chronological chart showing bathymetric ranges of various formations from the Valiente Peninsula, Popa Island, Cayo Agua, and the southern Limón and Panama Canal basins. Dashed lines enclose the same geologic section. Dotted lines show the biochronologic ranges of sections that are placed according to physical stratigraphy.

FIG. 10. A. Schematic paleogeographic reconstruction of the Panamanian Isthmus at 15-16 Ma. Circles represent reliably dated sections that have yielded rich benthic foraminiferal assemblages useful for paleobathymetric analysis. The Central Cordilleran Volcanic Arc is shown as a line of islands; the triangles represent volcanoes. Evidence of middle Miocene volcanism in western Panama is from de Boer et al. (1988, 1991) and references therein. Land areas to the south of the arc are interpreted as exotic terrains. The Panamanian Isthmus at this stage was a volcanic island arc with a narrow neritic zone. The Southern Limón and Bocas del Toro Basin sediments indicate bathyal paleodepths in contrast to the Panama Canal Basin where neritic to emergent condition persist through most of the Cenozoic. B: Schematic paleogeographic reconstruction of the Panamanian Isthmus at 11-12 Ma. Symbols as for part A. The neritic zone has by this time expanded significantly and an emergent active volcanic back-arc has developed in the Bocas del Toro Basin. We assume that the Central Cordilleran volcanic arc had become emergent at this time.


A
15-16Ma
Southern Limon Basin
CARIBBEAN SEA
Panama Canal Basin
Bocas del Toro Basin
COST A RICA
PANAM A
PACIFIC OCEAN
N
0 Km 100
land
neritic
bathyal
Azuero Peninsula
B
11 -1 2 M a
CARIBBEAN SEA
Southern Limon Basin
Panama Canal Basin
Bocas del Toro Basi n
COST A RICA
PANAM A
N
0 Km 100
PACIFIC OCEAN
land
neritic
bathyal
Azuero Peninsula

back-arc, parallel to the main Central Cordilleran arc. The environment of the Bocas del Toro back arc archipelago, by 12 Ma, had patchy shallow-water fringing reefs around active volcanic islands whose emergent flanks were characterized by laharic breccia and basalt flows. The lahars and flows graded laterally into fluviatile and deltaic sequences, and then into resedimented near-shore deposits. Major volcanic activity in the area ceased about 12 Ma (the youngest radiometric date on columnar basalt flows,) although there are younger basalt dykes intruding the Valiente Formation sediments, e.g., at Laurel point, Isla Popa (Fig. 4), dated about 8.5 Ma.

To the northwest, in the southern Limón Basin, a similar general shallowing pattern is observed (Coates et al. 2004, Fig. 9). From ~18-13 Ma, the Uscari Formation shallows from middle bathyal (1000-600 m) to outer neritic (100-200 m) depths. The record is absent after 13 Ma. The Gatun Formation (11.8-11.4 Ma) an inner neritic (<50 m) deposit in the Panama Canal Basin (Collins et al., 1996a) is evidence that the emergence of the isthmus had developed to a similar degree in that region. In the central Darien region (Coates et al. 2004), middle Miocene deposits shallowed from middle bathyal depths (1000-600 m) in the Clarita and Tapaliza formations (~16.4-11.2 Ma) to neritic depths (<200 m) in the Tuira, Yaviza, and Chucunaque formations (11.2-5.6 Ma).

In the Bocas del Toro region, the Valiente Formation is unconformably overlain by the Tobobe Sandstone Formation (Coates et al. 1992; Coates 1999), indicating flooding of the eroded extinct volcanic arc rocks by very shallow water. Deposition of the marginal marine conglomerate and sandstone signals the start of a marine transgressive/regressive cycle (Fig. 9). Sediments of the conformably overlying Nancy Point Formation (Messinian 7.26-5.32 Ma; Aubry and Berggren 1999) show that deepening proceeded to upper bathyal depths (200-600 m; Collins 1993). This deepening is also recorded in the Panama Canal Basin (Coates et al. 2004, Fig. 9) where a rapid transition occurs from the inner neritic (20-40 m), middle-upper Gatun Formation (~11-8 Ma) to the overlying upper bathyal (200-600 m) Chagres Formation (~6 Ma; Collins et al. 1996a). It is not clear whether deepening represents a eustatic (sea level) or a regional tectonic event caused by cooling and sinking of the Bocas del Toro volcanic arc.

By the early Pliocene (Zanclean, 5.2-3.5 Ma), marine regression had caused rapid shallowing throughout the Bocas del Toro Basin (Shark Hole Point and Cayo Agua formations). Coeval deposits (4-1 Ma) in the southern Limón Basin (Rio Banano, Quebrada Chocolate, Moin, and Suretka formations) also record rapid shallowing and emergence (McNeill et al. 2000). Similarly, shallowing to neritic (<100 m) or emergent conditions was occurring in the Darien region (Yaviza Formation, Tuquesa and Chucunaque formations; Coates et al. 2004). These patterns are evidence of the shoaling of Central American isthmus volcanic arc (4.7-2.8 Ma). In the Northern Region of the Bocas del Toro archipelago there is an extensive Plio-Pleistocene sequence, ranging in age from about 3.5 to 0.78 Ma, that displays a widespread development of coral reef formation. This is in marked contrast to the very limited coral reef lenses intercalated into the siliciclastic Miocene sediments the Southern Region. Collins et al. (1996b) have demonstrated the increase, from the late Miocene, of carbonate dwelling benthic foraminiferal species and of corals associated with increased warming and salinity (and decreased productivity) in the western Caribbean as a result of closure of the Isthmus of Panama. The Northern Region of the Bocas del Toro archipelago demonstrates the same trend.

Conclusions

1) Prior to the collision of the southern Central American arc with south America, upper Cretaceous to lower Miocene rocks of the Bocas del Toro Basin (lower Miocene, Punta Alegre Formation) were deposited in abyssal to lower bathyal depths in an open-ocean, low-energy, essentially non-siliciclastic sedimentary environment distant from South America.
2) The Valiente Formation records the

rapid growth of an active volcanic arc which by ~12 Ma was an extensive emergent archipelago of volcanic islands flanked by coral reefs.

3) After a prolonged period of emergence and erosion, marine sediments began to cover the extinct volcanic arc starting about 7.2-5.3 Ma.
4) The deposits of this transgressive/regressive marine cycle are named the Bocas del Toro Group. The oldest units (Tobobe Sandstone and Nancy Point Formation), record deepening to 200 m. The younger units (Shark Hole Point, Cayo Agua, and Escudo de Veraguas formations) represent the regressive sequence.
5) In the Plio-Pleistocene, an extensive coral reef system developed either on a basement of siliciclastic sediments (Colon Island, Swan Cay) or on the basalt of the Miocene Valiente Formation (Bastimentos Island), reflecting the oceanographic changes taking place in the western Caribbean as a result of shallowing and closure of the Isthmus of Panama.

Acknowledgments.—This research was supported by the National Science Foundation grants BSR-9006523, DEB-9696123 and DEB-9705289 to AGC, LSC, and Jeremy Jackson; several grants from the National Geographic Society to AGC and LSC, and Scholarly Studies and Walcott Fund awards from the Smithsonian Institution to AGC. We are grateful to the staff of the STRI field station in Bocas del Toro and to numerous field assistants of the Panama Paleontology Project, who have helped with the complex logistics of fieldwork in this region since 1986 (see Collins and Coates, 1999 for details), but particularly to Beatrice, Lucien Ferrenbach and Doroteo Machado, and whose constant efforts to maintain motors and vessels, and to organize food and gasoline, allowed us to work with maximum efficiency. We are also very grateful to Xenia Saavedra for laboratory technical and logistical support, including organizing (and sometimes preparing) samples, tracking them in the data base, producing field maps, and numerous other tasks. Janet Coates, Gloria Jovane, Lidia Mann, Isis Estribi, and the crews of the RV Benjamin and RV Urracca provided invaluable logistical support over many years. We also thank Rachel Collin, Ann Budd, and Aaron Odea for very helpful reviews.

Literature Cited

Astorga, A., et al. 1991. Cuencas sedimentarias de Costa Rica: Evolución geodinámico y potencial de hidrocarburos. *Rev. Geol. Am. Central* 13:25-59.

Aubry, M-P., and W. A. Berggren. Newest Biostatigraphy. 1999. Appendix 1, In *A Paleobiotic Survey of Caribbean Faunas from the Neogene of the Isthmus of Panama*, ed. L.S. Collins, and A. G. Coates, 38-40, *Bull. Am. Paleontol.*, No. 357.

Berggren, W.O., D. V. Kent, C. C. Swisher, and M-P. Aubry. 1995. A revised geochronology and chronostratigraphy. In *Time scales and Global Stratigraphic Correlation*, ed. W. A. Berggren, D. V. Kent, M-P. Aubry and J. Hardenbol, 129-212, *Society of Economic Paleontologists and Mineralogists Special Volume*, No. 54.

Bottazzi, G., J. A. Fernandez, and G. Barboza. 1994. Sedimentología e historia tectonosedimentaria de la cuenca Limón Sur. *Profi,* 7:351-391.

Burke, K. and A.M.C. Senghor. 1986. Tectonic escape in the evolution of the continental crust. In *Reflection seismology: The continental Crust* ed. M. Barazangi, and L.D. Brown, 41-53, *Am. Geophys. Union Geodynamics Ser.*, 14:41-53, Washington D.C.

Budd, A.F. and K.G. Johnson. 1997. Coral reef community dynamics over 8 million years of evolutionary time: stasis and turnover. *Proc. 8th Internat. Coral Reef Symp., Panama*, 423-428.

Budd, A.F. and K.G. Johnson. 1999. Origination preceding extinction during Late Cenozoic turnover of Caribbean reefs. *Paleobiology* 25:188-200.

Case, J.E., W.D. MacDonald, and P.J. Fox. 1990. Caribbean crustal provinces. In *The Geology of North America*, ed. G. Dengo and J.E. Case, 15-36, vol. H, *The Caribbean Region. Decade of North American Geology, Geological Society of America, Boulder, Colorado*.

Cassell, D.T. and B.K. Sen Gupta. 1989. Foraminiferal stratigraphy and paleoenvironments of the Tertiary Uscari Formation, Limón Basin, Costa Rica, *J. Foram. Res.*, 19:52-71.

Coates, A.G. 1999. Lithostratigraphy of the Neogene strata of the Caribbean coast from Limon, Costa Rica to Colon, Panama. In *A paleobiotic survey of Caribbean faunas from the Neogene of the Isthmus of Panama*, ed. L.S. Collins, and A.G. Coates, 15-36. *Bull. Am. Paleontol.,* No. 357.

Coates, A.G. and J. A. Obando. 1996. The geologic evolution of the Central American isthmus. In *Evolution and environment in tropical America*, ed. J.B.C. Jackson, A.F. Budd, and A.G. Coates, 21-56, *University of Chicago Press, Chicago*.

Coates, A.G., J.B.C. Jackson, L.S. Collins, T.M. Cronin, H.J. Dowsett, L.M. Bybell, P. Jung, and J.A. Obando, 1992, Closure of the Isthmus of Panama: the near-shore marine record of Costa Rica and western Panama. *Geol. Soc.Am. Bull.*, 104:814-828.

Coates, A.G., M-P. Aubry, W.A. Berggren, L.S. Collins, and M. Kunk. 2003. Early history of the Central American arc from Bocas del Toro, western Panama. *Geol. Soc. Am. Bull.*, 115:271-287.

Coates, A.G., Collins, M-P. Aubry, W.A. Berggren. 2004. The Geology of the Darien, Panama, and the late Miocene-Pliocene collision of the Panama arc with northwestern South America. *Geol. Soc. Am. Bull.*, 116:1327-1344.

Collins, L.S. 1993. Neogene paleoenvironments of the Bocas del Toro Basin, Panama. *J. Paleontol.*, 67:699-710.

Collins, L.S. and A.G. Coates, Ed. 1999. A paleobiotic survey of Caribbean faunas from the Neogene of the Isthmus of Panama. *Bull. Am. Paleontol.*, 357:1-351.

Collins, L.S., A.G. Coates, J.B.C. Jackson, and J.A. Obando. 1995. Timing and rates of emergence of the Limón and Bocas del Toro basins: Caribbean effects of Cocos Ridge subduction? In *Geologic and tectonic development of the Caribbean plate boundary in southern Central America*, ed. P. Mann, 263-289, *Geol. Soc. Am., Spec. Pap.*, No. 295.

Collins, L.S., A.G. Coates, W.A. Berggren, M-P. Aubry, and J. Zhang. 1996. The late Miocene Panama isthmian strait. *Geology*, 24:687-690.

Collins, L.S., A.F. Budd, and A.G. Coates. 1996. Earliest evolution associated with closure of the Tropical American Seaway. *Proc. Nat. Acad. Sci.*, 93:6069-6072.

Collins, L.S., O. Aguilera, P.F. Borne, and S.D. Cairns. 1999. A paleoenvironmental analysis of the Neogene of Caribbean Panama and Costa Rica using several phyla. In *A Paleobiotic Survey of Caribbean Faunas from the Neogene of the Isthmus of Panama*, ed. L.S. Collins, and A.G. Coates, 81-87, *Bull. Am. Paleontol.* No. 357.

de Boer, J.Z., M.J. Defant, R.H. Stewart, J.F. Restrepo, L.F. Clark, and A.H. Ramirez. 1988. Quaternary calc-alkaline volcanism in western framework. *J. S. A. Earth Sci.*, 1:275-293.

Donnelly, T.W., G.S. Horne, R.C. Finch, and E. Lopez-Ramos. 1990. Northern Central America; the Maya and Chortis blocks. In *The Geology of North America*, ed. G. Dengo, and J.E. Case, 37-76, *vol. H, The Caribbean Region*, *Geological Society of America, Boulder, Colorado*.

Duque-Caro, H. 1990. Neogene stratigraphy, palaeoceanography and palaeobiogeography in northwest South America and the evolution of the Panama Seaway. *Palaeogeogr. Palaeoc. Palaeoecol.*, 77:203-234.

Gussone, N., A. Eisenhauer, R. Tiedemann, G.H. Haug, A. Heuser, B. Bock, Th.F. Nagler, and A. Muller. 2004. Reconstruction of Caribbean Sea surface temperatures and salinity fluctuations in response to the Pliocene closure of the Central American Gateway and radiative forcing using $\delta^{44/40}$Ca, δ^{18}O and Ca/Mg ratios. *Earth Planet. Sci. Lett.*, 227:201-214.

Jackson, J.B.C., and L. D'Croz. 1999. The Ocean Divided. In *Central America, A Natural and Cultural History*, ed. A.G. Coates, 38-71, *Yale University Press, New Haven*.

Jackson, J.B.C., J. Jung, A.G. Coates, and L.S. Collins. 1993. Diversity and extinction of tropical American mollusks and emergence of the Isthmus of Panama. *Science*, 260:1624-1626.

Haug, G.H. and R. Tiedemann. 1998. Effect of the formation of the Isthmus of Panama on Atlantic Ocean thermohaline circulation. *Nature*, 393:673-676.

Keigwin, L.D. 1982. Isotopic paleoceanography of the Caribbean and East Pacific: role of Panama uplift in late Neogene time. *Science*, 217:350-352.

Kolarsky, R.A., P. Mann, and W. Montero. 1995. Island arc response to shallow subduction of the Cocos Ridge, Costa Rica. In *Geologic and tectonic development of the Caribbean plate boundary in southern Central America*, ed. P. Mann, 235-262, *Geol. Soc. Am. Spec. Pap.* 295.

Mann, P. and R.A. Kolarsky. 1995. East Panama deformed belt: Structure, age, and neotectonic significance. In *Geologic and tectonic development of the Caribbean plate boundary in southern Central America*, ed. P. Mann, 111-130, *Geol. Soc. Am. Spec. Pap.* 295. McNeill, D.F., A.G. Coates, A.F.Budd, and P.F. Borne, 2000, Integrated biological and paleomagnetic stratigraphy of Late Neogene deposits around Limón, Costa Rica: a coastal emergence record of the Central American Isthmus. *Geol. Soc. Am. Bull.*, 112:963-981.

Silver, E.A., D.L. Reed, J.E. Tagudin, and D.J. Heil. 1990. Implications of the north and south Panama deformed belts for the origin of the Panama orocline. *Tectonics*, 9:261-282.

Webb, S.D. 1999. The Great American Faunal Interchange. In *Central America, A Natural and Cultural History*, ed. A.G. Coates, 97-122, *Yale University Press, New Haven.*

Webb, S.D. and A. Rancy. 1996. Late Cenozoic Evolution of the Neotropical Mammal Fauna. In *Evolution and Environment in Tropical America*, ed. J.B.C. Jackson, A.F. Budd, and A.G. Coates, 335-358. *The University of Chicago Press, Chicago*.