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Fossil Corals from the Gulf of California, México: Still a Depauperate Fauna but it Bears More Species than Previously Thought

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A new collection of fossil hermatypic corals from the late Miocene Imperial Formation, the early Pliocene San Marcos Formation, the middle to late Pliocene Carmen Formation and the Pleistocene, Gulf of California, Mexico, has yielded four undescribed species *Siderastrea* sp., *cf. Placosmilia* sp., *Favia* sp. 1., and *Favia* sp. 2. Additionally, new occurrences of the previously described *Pocillopora damicornis* (Linnaeus 1758), *Pocillopora verrucosa* (Ellis and Solander 1786), *Pocillopora meandrina* Dana 1846, *Gardineroseris planulata* (Dana 1846), *Pavona clavus* (Dana 1846), *Porites lobata* Dana 1846, *Diploria sarasotana* Weisbord 1974 as well as *Dichocoenia eminens* Weisbord 1974, are reported. The fauna occurs either in low-angle ramps or flatlying terraces of variable extension. Most outcrops are small, and reminiscent of more extensive deposits usually deposited on open, exposed, high-energy environments. However, well preserved units deposited on protected embayments are also present. Except at Isla Coronados and La Ventana where multiple coral terraces occur, coral bearing units represent single spatio-temporal growth episodes. The present analysis shows that hermatypic coral fauna between late Miocene to late Pleistocene in the Gulf of California is still depauperate; nonetheless it bears many more species than previously thought.

KEY WORDS: Checklist, fossils, corals, distribution, Gulf of California

Fossil reef corals have previously been reported from the eastern Pacific during the Cenozoic where up to 151 coral species, including synonyms, have been recorded (López-Pérez 2005). Between the late Miocene and Recent time fossil-bearing units are spatially restricted to the Gulf of California, and there is a lack of outcrops in western México and Central America (Palmer 1928; Hertlein 1972). Since in 1893 Fairbanks first recorded the existence of an unusually interesting coral fauna from Imperial Valley, California, thirteen species included in nine genera have been reported in the Gulf of California area; surprisingly those coral taxa were treated in a handful of papers published by Vaughan (1917), Durham (1947, 1950), and Squires (1959). The rest of the Gulf of California literature has just added fossiliferous localities to the record (Jordan and Hertlein 1926; Hertlein 1957; Hertlein and Emerson 1959; Emerson 1960; Emerson and Hertlein 1964; Hertlein 1966; Simian and Johnson 1997; Johnson and Ledesma-Vázquez 1999; Gastil et al. 1999; De Diego-Forbis et al. 2004). As demonstrated by the present paper, rather than being caused by the impoverished and to some extent homogenous fauna of the Gulf of California, the pattern mainly resulted from the focus of the studies; except for the works of Vaughan (1917), Durham (1947,

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1950) and Squires (1959), whose main concern was hermatypic corals, most reports were incidental in nature and resulted from studies focused on aspects other than corals.

An interinstitutional and multidisciplinary research team is targeting Pliocene to Pleistocene coral communities in the Gulf of California in order to assemble a detailed geologic and taxonomic framework for already known and new coral bearing units. The focus of the present paper is to report new records of fossil corals from the late Miocene to late Pleistocene in the Gulf of California, to provide basic information on the lithology, age and paleoenvironment of each unit where fossil corals were collected, and to discuss some distribution aspects. Further implications in paleoecology, paleogeography and evolution of the group in the Gulf of California will be discussed elsewhere.

Stratigraphy and Geologic Setting

The fauna described below was collected from late Miocene to late Pleistocene fossil coral outcrops showing reef development in the Gulf of California area (Fig. 1). A general account of the nature and deposition of the coral bearing units is followed by a brief synopsis of the lithology, age, and paleoenvironment of each unit. Information regarding locality, geologic formation, age and collected species is detailed in Table 1.

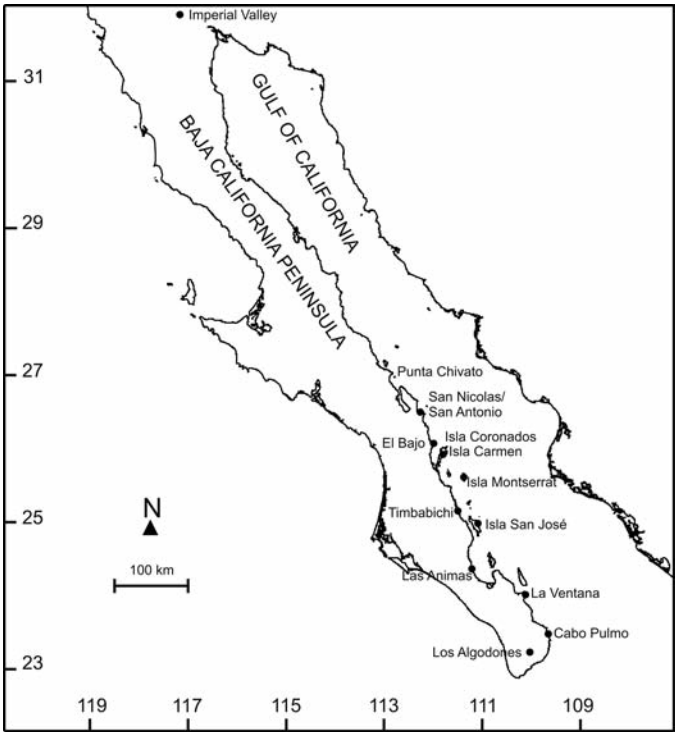

FIGURE 1. Study localities in the Gulf of California, northwestern México. Each dot represents a general area, detailed information about each locality is listed in Table 1.

Coral-bearing units.— Coral-bearing units form low-angle ramps (Punta Chivato area, San Nicolas, Isla Montserrat; Fig. 1; Table 1), or flat-lying terraces (Isla Coronados, Las Animas, Cabo Pulmo; Fig. 1; Table 1) of variable extension. They usually rest with an angular unconformity on the tilted volcanics of the Miocene Comondú Group in the Bahía Conception area (Ledesma-Vázquez and Johnson 2001), Miocene El Cien Formation at Las Animas (DeDiego-Forbis et al. 2004), and early Pliocene Trinidad Formation at Rancho Algodones (Martínez-Gutiérrez and Sethi 1997). Most outcrops are small, reminiscent of more extensive deposits, which are usually deposited on open, exposed, high-energy environments; however, well preserved units deposited in protected embayments are also presented (South Punta Chivato, Cañada Coronados, Puerto Balandra, Las Animas; Fig. 1; Table 1). Marine deposits are common and widespread from Santa Rosalia to Cabo Pulmo (Ortlieb 1991), although those recording reef development are scarce. Except at Isla Coronados (Johnson et al. 2007) and La Ventana where multiple coral terraces occur, they represent single spatio-temporal growth episodes. Finally, in contrast with the Indo-Pacific and Caribbean where coral accumulations have a wide bathymetric range (~ 0–50 m) and therefore most reef-building episodes preserve several reef environments (Pandolfi 1996), Gulf of California coral communities developed in shallow water (<15 m) and coral-bearing units generally represent single reef environments.

Imperial Formation.— The Imperial Formation is a lithologic unit described from the Coyote Mountains in Southern California (Hanna 1926) and deposited in the "pull-apart" basin of the Salton trough (Fig. 2). In general, the Imperial Formation overlies Mesozoic and older metamorphic basement at contacts representing rocky shorelines containing marine borings, and is covered predominantly with Quaternary age sediments (Watkins 1990). The Imperial Formation unconformably overlies the Alverson Formation and local non-marine units, and represents marine conditions consisting of green micaceous shale, calcareous sandstone and yellow biostromal claystone (Kidwell 1988). Corals were collected by Ann F. Budd (Department of Geoscience, University of Iowa) from the calcareous sandstone Latrania Member at Barrett Canyon, northeast of Coyote Mountains and Alverson Canyon (Fig. 2; Table 1), deposited under shallow marine conditions (Foster 1979, 1980). A more detailed analysis regarding the stratigraphic setting of the collecting localities is provided by Foster (1979, 1980).

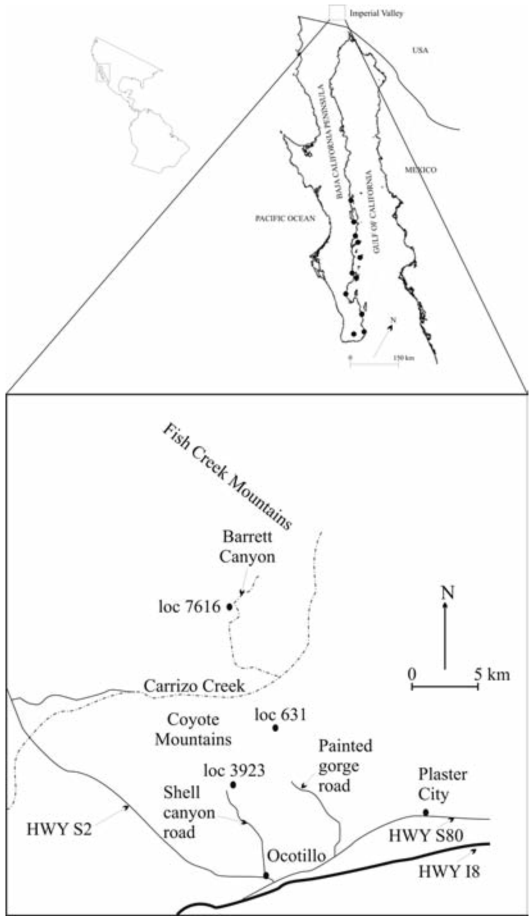

Figure 2. Collecting localities in the late Miocene Imperial Formation of California, United States. Detailed information about each locality is listed in Table 1. Adapted from Foster (1979).

Studies indicate that the boundary between members of the formation is time-transgressive and that the unit includes multiple biofacies of uncertain temporal relations. However, radiometric ages from rocks overlying and underlying fossiliferous facies constrain the age of the Imperial Formation to greater than 6 Ma and less than 6.5 Ma (Eberly and Stanley 1978, for rocks underlying the Imperial Formation in the Coyote Mountains; McDougall et al. 1999, for rocks overlying the Imperial Formation in Whitewater Canyon).

San Marcos Formation.— The San Marcos Formation is the lower member of a much larger lithologic unit referred as the Salada Formation by the Marland Oil Company (Anonymous 1924) used to describe all the marine Pliocene of Baja California. As designated by Anderson (1950), the San Marcos Formation overlies unconformably tilted Oligocene to Miocene andesites, basalts, tuffs and volcanic breccias of the Comondú group (McFall 1968). The San Marcos Formation is a sequence of clastic sediments, gypsum and pebbly limestone at San Marcos Island, but consists of ~ 61 m of volcanic gravels, sandstones, and siltstones at Isla Carmen (Anderson 1950).

Corals were collected from a pebbly limestone facies to the north of Punta Chivato and Ensenada El Muerto in the Punta Chivato area, and calcareous sandstone at Puerto de la Lancha in Isla

TABLE 1. Locality and taxa register. Global positioning satellite co-ordinates taken between June 2002 and January 2005 are given for each locality. * = New records.

BC 1, South Punta Chivato; elevation 6 m; N 27°04.382′–W 111°57.558′. Geologic age: late Pleistocene, 117.9 ± 0.6 ky. Faunal list: *Porites panamensis*.

BC 2, Las Barracas; elevation 49 m; N 27°03.262′–W 111°59.953′. Formation: Marquer. Geologic age: middle to late Pliocene. Faunal list: *Porites carrizensis*, *Dichocoenia merriami*.

BC 3, Punta Chivato; elevation 70 m; N 27°05.537′–W 111°57.511′. Formation: San Marcos. Geologic age: early Pliocene. Faunal list: *Porites carrizensis*, *Solenastrea fairbanksi*, * *cf. Placosmilia* sp.

BC 4, San Nicolas; elevation 72 m; N 26°31.559′–W 111°34.068′. Formation: San Nicolas. Geologic age: middle to late Pliocene, < 3.3 ± 0.5 Ma. Faunal list: * *cf. Placosmilia* sp.

BC 5, San Antonio; elevation 28 m; N 26°31.771′–W 111°28.153′. Geologic age: late Pleistocene, 130–120 ky. Faunal list: *Porites panamensis.*

BC 6, Las Animas 1; elevation 17 m; N 24°32.447′–W 110°44.290′. Geologic age: late Pleistocene, 130–128 ky. Faunal list: *Porites panamensis*, *Pocillopora capitata.*

BC 7, Las Animas 2; elevation 27 m; N 24°32.642′–W 110°44.372′. Geologic age: late Pleistocene, 130–128 ky. Faunal list: *Porites panamensis*, *Pocillopora capitata*.

BC 8, Cabo Pulmo; elevation 32 m; N 23°26.186′–W 109°25.700′. Geologic age: late Pleistocene, 140–120 ky. Faunal list: *Porites panamensis,* **Porites lobata*, *Pocillopora capitata*, **Pocillopora meandrina*, **Pocillopora damicornis*.

BC 9, Rancho Los Algodones; elevation 149 m; N 23°12.767′–W 109°39.858′. Formation: El Refugio. Geologic age: early Pliocene. Faunal list: *Solenastrea fairbanksi*.

BC 10, La Ventana1; elevation 3 m; N 24°02.520–W 109°49.432′. Geologic age: late Pleistocene. Faunal list: *Porites panamensis*, *Pocillopora capitata,* **Pocillopora damicornis*, **Pavona clavus*.

BC 11, La Ventana 2; elevation 15 m; N 24°01.922′–W 109°48.853′. Geologic age: middle Pleistocene. Faunal list: *Porites panamensis*, *Pocillopora capitata*, **Pavona clavus*, **Gardineroseris. planulata*, *Psammocora stellata*.

BC 12, Punta Baja, Isla Carmen; elevation 16 m; N 25°49.009′–W 111°12.526′. Geologic age: late Pleistocene. Faunal list: *Porites panamensis, Porites sverdrupi*, *Pocillopora capitata*, *Psammocora stellata*.

BC 13, South Isla Carmen; elevation 10 m; N 25°49.139′–W 111°12.870′. Geologic age: late Pleistocene. Faunal list: *Porites panamensis*.

BC 14, Arroyo Blanco, Isla Carmen; elevation 79 m; N 25°53.759′–W 111°11.526′. Geologic age: Pleistocene. Faunal list: *Porites panamensis*.

BC 15, Puerto de la Lancha, Isla Carmen; elevation 30 m; N 26°03.284′–W 111°06.372′. Formation: San Marcos. Geologic age: early Pliocene. Faunal list: *Porites panamensis*, *Porites carrizensis*, *Solenastrea fairbanksi*, **Siderastrea* sp., **Favia* sp. 2.

BC 16, Bahía Oto, Isla Carmen; elevation 7 m; N 26°02.550′–W 111°09.730′. Formation: Carmen. Geologic age: middle to late? Pliocene, 3.1–1.8 Ma. Faunal list: *Porites panamensis*.

BC 17, Puerto Balandra 1, Isla Carmen; elevation 2 m; N 26°01.395′–W 111°09.960′. Geologic age: late Pleistocene. Faunal list: *Porites panamensis*.

BC 18, Puerto Balandra 2, Isla Carmen; elevation 1 m; N 26°00.949′–W 111°09.843′. Geologic age, late Pleistocene. Faunal list: *Porites panamensis*.

BC 19, Bahía Marquer, Isla Carmen; elevation 26 m; N 25°52.748′–W 111°13.033. Formation: Marquer. Geologic age: middle? to late Pliocene. Faunal list: *Porites panamensis*.

BC 20, Timbabichi; elevation 5 m; N 25°16.756′–W 110°56.004′. Geologic age: late Pleistocene. Faunal list: *Porites panamensis*, *Pocillopora capitata*, **Pocillopora damicornis*, *Pocillopora elegans*, **Pocillopora verrucosa*.

BC 21, Sur Timbabichi; elevation 11 m; N 25°14.383′–W 110°56.509′. Geologic age: late Pleistocene. *Porites panamensis*.

BC 22, Isla San José 1; elevation 56 m; N 25°01.168′–W 110°35.172′. Geologic age: middle Pliocene. Faunal list: *Dichocoenia merriami*.

BC 23, Isla San José 2; elevation 105 m; N 25°00.737′–W 110°34.856′. Geologic age: middle Pliocene. Faunal list: *Solenastrea fairbanksi*, **Diploria bowersi*.

BC 24, Isla Montserrat 1; elevation 43 m; N 25°39.810′–W 111°02.384′. Formation: San Marcos. Geologic age: early Pliocene. Faunal list: *Porites panamensis*.

BC 25, Isla Montserrat 2; elevation 204 m; N 25°40.379′–W 111°01.880′. Formation: Carmen. Geologic age: middle to late? Pliocene. Faunal list: *Porites carrizensis*, *Pocillopora capitata*, **Favia* sp. 1.

BC 26, Isla Montserrat 3; elevation 213 m; N 25°40.470′–W 111°01.837′ Formation: Carmen. Geologic age: middle to late? Pliocene. Faunal list: *Porites carrizensis*, *Pocillopora capitata*, **Favia* sp. 1.

BC 27, Isla Montserrat 4; elevation 202 m; N 25°40.520′–W 111°01.784′ Formation: Carmen. Geologic age: middle to late? Pliocene. Faunal list: *Porites carrizensis*, *Pocillopora capitata*, **Favia* sp. 1.

BC 28, La Ventana 3; elevation 15 m; N 24°02.474′–W 109°49.577′. Geologic age: middle? Pleistocene. Faunal list: *Porites panamensis*.

BC 29, La Ventana 4; elevation 21 m; N 24°02.200′–W 109°49.332′. Geologic age: middle? Pleistocene. Faunal list: *Porites panamensis*.

BC 30, La Ventana 5; elevation 19 m; N 24°02.033′–W 109°49.175′. Geologic age: middle? Pleistocene. Faunal list: *Porites panamensis*, **Pavona clavus*.

BC 31, La Ventana 6; elevation 39 m; N 24°01.947′–W 109°49.160′. Geologic age: early? Pleistocene. Faunal list: *Porites panamensis*, **Pavona clavus.*

BC 32, La Ventana 7; elevation 54 m; N 24°01.834′–W 109°49.130′. Geologic age: early Pleistocene. Faunal list: *Porites panamensis*, **Pavona clavus.*

BC 33, Las Animas 3; elevation 17 m; N 24°32.672′–W 110°44.358′. Geologic age: late Pleistocene. Faunal list: *Porites panamensis*, *Pocillopora capitata*, * *Pocillopora damicornis*, *Psammocora stellata*.

BC 34, El Bajo; elevation 10 m; N 26°06.085′–W 111°19.626′. Geologic age: late Pleistocene. Faunal list: *Porites panamensis*.

BC 35, Ensenada El Muerto; elevation 19 m; N 27°05.722′–W 111°58.797′. Formation: San Marcos. Geologic age: early Pliocene. Faunal list: *Porites panamensis*, *Porites carrizensis*, *Dichocoenia merriami*, **Dichocoenia eminens*, *Solenastrea fairbanksi*, * *cf. Placosmilia* sp., **Diploria sarasotana*.

BC 36, Isla Coronados 1; elevation 9.8 m; N 26°06.718′–W 111°16.670′. Geologic age: late Pleistocene. Faunal list: *Porites panamensis*, *Pocillopora capitata*.

BC 37, Isla Coronados 2; elevation 11.95 m; N 26°06.719′–W 111°16.665′. Geologic age: late Pleistocene. Faunal list: *Porites panamensis*, *Psammocora stellata*.

BC 38, Cañada Coronados, Isla Coronados; elevation 12–14 m; N 26°06.563′–W 111°16.376′. Geologic age: late Pleistocene. Faunal list: *Porites panamensis*, **Pavona clavus*, *Pavona gigantea*.

BC 39, Isla Coronados 4; elevation 16 m; N 26°06.620′–W 111°16.352′. Geologic age: middle Pleistocene. Faunal list: *Porites panamensis*, *Pocillopora capitata*.

BC 40, Isla Coronados 5; elevation 17.5 m; N 26°06.502′–W 111°16.198′. Geologic age: middle? Pleistocene. Faunal list: *Porites panamensis*, *Pocillopora capitata*.

BC 41, Isla Coronados 6; elevation 19.5 m; N 26°06.499′–W 111°16.165′. Geologic age: middle? Pleistocene. Faunal list: *Porites panamensis*, *Pocillopora capitata*, *Pocillopora elegans*, *Pavona gigantea*.

BC 42, Isla Coronados 7; elevation 22.5 m; N 26°06.708′–W 111°16.158′. Geologic age: middle? Pleistocene. Faunal list: *Porites panamensis*, *Pocillopora capitata*.

BC 43, Isla Coronados 8; elevation 23.95 m; N 26°06.713′–W 111°16.164′. Geologic age: middle? Pleistocene. Faunal list: *Porites panamensis*.

BC 44, Isla Coronados 9; elevation 24.25 m; N 26°06.717′–W 111°16.169′. Geologic age: middle? Pleistocene. Faunal list: *Porites panamensis*.

USGS 07616, Barret Canyon (Vaughan 1917; Foster 1979). Formation: Imperial. Geologic age: late Miocene. Faunal list: *Porites carrizensis*, *Dichocoenia merriami*, *Solenastrea fairbanksi*, *Siderastrea mendenhalli*.

UCLA 631, northeast Coyote Mountains (Foster 1979). Formation: Imperial. Geologic age: late Miocene. Faunal list: *Porites carrizensis*, *Dichocoenia merriami*, **Dichocoenia eminens*, *Solenastrea fairbanksi*, *Siderastrea mendenhalli*, *Diploria bowersi*.

USGS 3923, Alverson Canyon (Vaughan 1917; Foster 1979). Formation: Imperial. Geologic age: late Miocene. Faunal list: *Porites carrizensis*, *Solenastrea fairbanksi*, *Siderastrea mendenhalli*, *Diploria bowersi*.

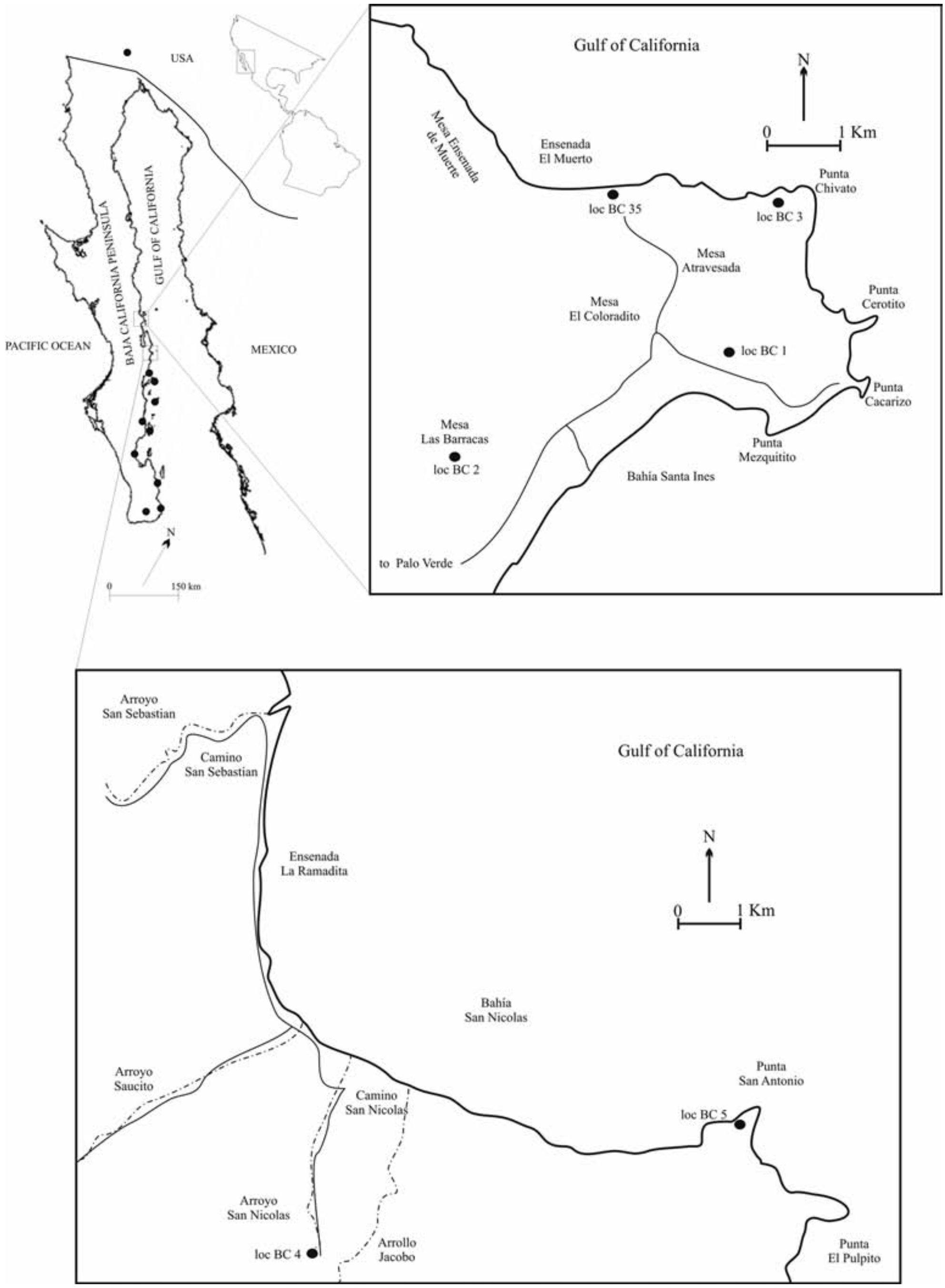

FIGURE 3. Collecting localities (●) at Punta Chivato and Bahía San Nicolas area in the Gulf of California, northwestern México. Detailed information about each locality is listed in Table 1. Adapted from Simian and Johnson (1997), and Ledesma-Vázquez (2002).

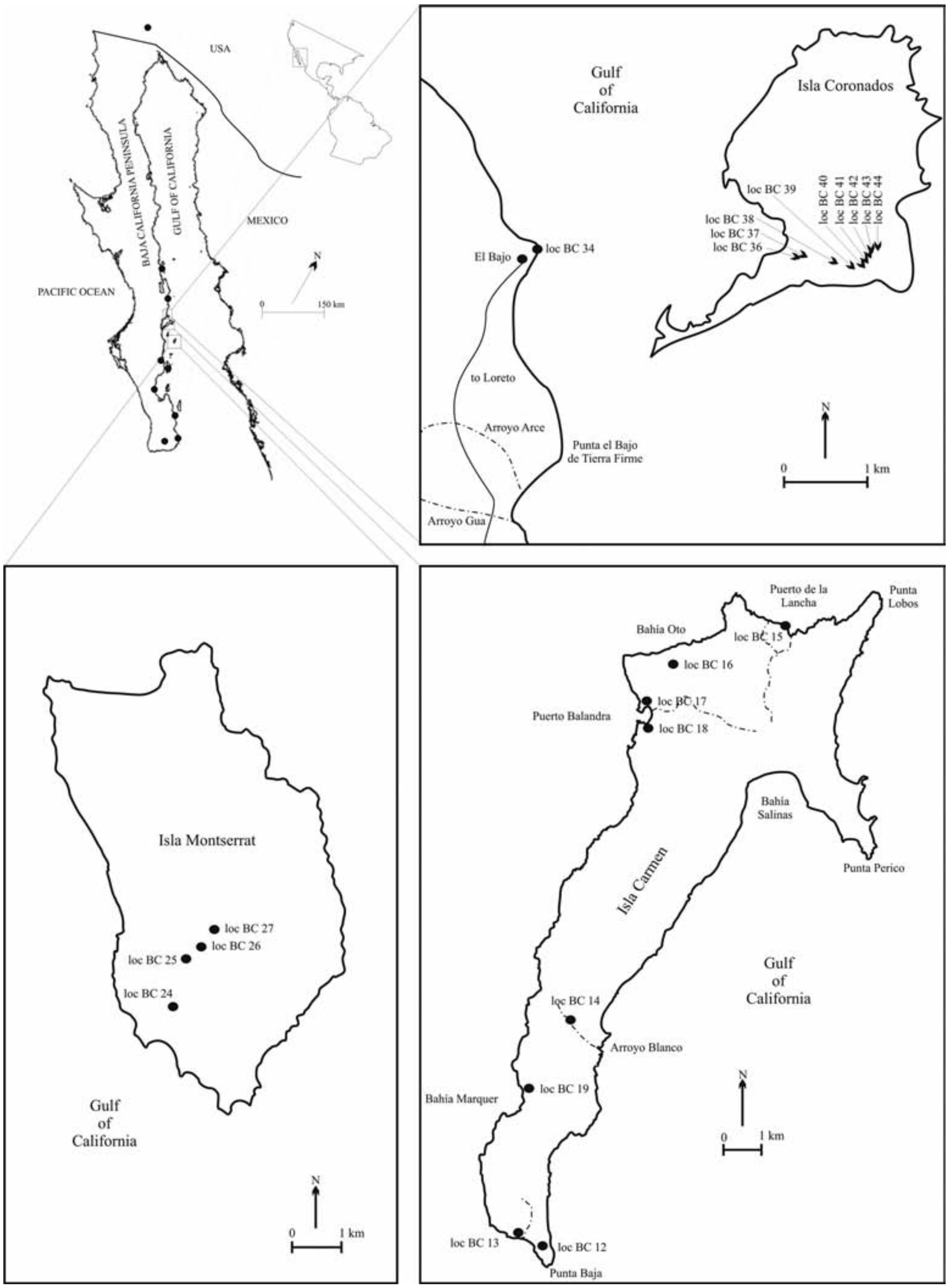

FIGURE 4. Collecting localities (•) at Coronados, Carmen and Montserrat Islands in the Gulf of California, northwestern México. Detailed information about each locality is listed in Table 1.

Carmen (Figs. 3 and 4; Table 1). The coral bearing units are relatively small at Puerto de la Lancha and north of Punta Chivato (Puerto de la Lancha, ~ 70 m in length with a maximum width of 15 m and a maximum height of 5 m; Punta Chivato, 107 m in length with a maximum width of 20 m and a maximum height of 1–4 m), but large at Ensenada El Muerto (greater than 500 m in length with a maximum width of 50–60 m and a maximum height of 5 m). At the localities, corals do not form a rigid reef structure; instead scattered colonies, which are poorly preserved, are mixed with andesite black pebbles in the Punta Chivato area. Based on the presence of index fossils (Durham 1950; Simian and Johnson 1997) and its relation with the Miocene Comondu Group, the coral facies were deposited under vigorous wave activity immediately after the Pliocene-Miocene unconformity during the early Pliocene.)

Carmen and Marquer Formations.— The Carmen Formation crops out around the eastern shore of Bahía Salinas and along the shore of Bahía Oto at Isla Carmen. Anderson (1950) defined the unit as ~ 460 m of volcanic pebble and cobble conglomerate, which is poorly bedded, and contains scattered interbeds of volcanic sandstone usually 0.3–0.7 m thick with fragmentary marine fossils. Dorsey et al. (2001) conducted a more detailed study of the sequence on the northeast side of Isla Carmen and found ~ 1200 m of thick bedded conglomerate, bedded conglomerate sandstone, bathyal marine marlstone and mudstone, dacite breccia, and conglomerate and bioclastic limestone. At Bahía Oto (Fig. 4), the Carmen Formation is a flat lying sequence formed by calcareous beds and volcanic conglomerate capped by light-gray limestone, where scattered intermediate-sized heads of massive *Porites panamensis* Verrill were collected. This section contains the upper conglomerate and youngest bioclastic unit identified at Punta Perico (Dorsey et al. 2001:100) and deposited in a high-energy marine-shelf setting. At Isla Montserrat (Fig. 4), the Carmen Formation is a unit ~ 12–34 m of basal conglomerate capped with light-gray fossiliferous limestone. *Pocillopora capitata* Verrill 1864, *Porites panamensis* Verrill 1866 and *Favia* sp1. collected at 200-220 m (Table 1) from the fossiliferous limestone do not form a reef structure; nonetheless colonies are abundant and not bound together and not attached to a firm substrate, but rather they are surrounded by Quaternary siliciclastics and Pliocene bioclastic sandstone.

The Marquer Formation is comprised of siliciclastic and bioclastic sediments, including calcareous conglomerates containing pebbles, calcareous sandstones, marls, coquina, algal limestone, and coral reef material (Anderson 1950). Most of the sediments, however, represent carbonate deposition accumulated in shallow marine environments (Durham 1950). Intermediate-sized heads (~ 7-10 cm height) of *Porites panamensis* were recovered from Bahía Marquer (Fig. 4; Table 1) formally designated as the type locality for the formation; here extensive reef (~ 140 m in length with a maximum width of ~ 92 m and a maximum height of ~ 3 m) composed of the above species form the upper part of the sequence. At Las Barracas (Fig. 3; Table 1), *Porites carrizensis* Vaughan 1917 was collected from the limestone (1–2 m) that caps the north/east corner of Mesa Las Barracas, whereas *Dichocoenia merriami* (Vaughan 1900) was collected from the thick (~ 36 m) unit of soft lime-rich siltstone underlying the limestone. Occurrence of the sand dollar *Encope shepherdi* Durham 1950 at Bahía Marquer and Las Barracas, suggests a late Pliocene age for the outcrops.

The age, lithology and faunal relationships between Carmen and Marquer formations are still not clear. The Carmen and Marquer formations were proposed by Anderson (1950) to represent middle and late Pliocene sequences, as suggested by the large-scale correlation of Durham (1950) based on mollusks; however, lithologically the beds closely resemble one another (Anderson 1950). Natland (1950) suggests a late Pliocene age for foraminiferal assemblages at Punta Perico, which is considered as the type locality for the Carmen Formation. This interpretation is further supported by Dorsey et al. (2001) who suggested a middle to late Pliocene age (~ 3.1–1.8 Ma) for the Carmen Formation based on planktonic foraminiferal stratigraphy. In addition, molluscan paleogeographic studies conducted by Smith (1991a, 1991b) indicate that mollusks are not effective at differentiating among formations. Further information is needed to determine the relative or absolute age of the outcrops.

San Nicolas Formation.— The San Nicolas Formation is a lithologic unit described from the Bahía Concepción area in Baja California Sur (Ledesma-Vázquez 2002). It was deposited during the crustal extension of the Proto-Gulf in the basin of San Nicolas. The San Nicolas Formation overlies the tilted Oligocene-Miocene Comondú Group, and represents marine conditions consisting of the lowermost Tobas San Antonio Member, the Los Volcanes alluvial fan, the transitional Lodolita Arroyo Amarillo Member, and the marine La Ballena Member (Johnson and Ledesma-Vázquez 2001; Ledesma-Vázquez 2002). A relatively large number of overturned specimens of the coral *cf. Placosmilia* sp. were collected from a fine sediment (mudstone) matrix not far above the Miocene-Pliocene unconformity (Fig. 3; Table 1). The matrix is mixed with abundant internal molds of a wide range of molluscan fossils belonging to the Arroyo Amarillo Member. According to Ledesma-Vázquez (2002), the maximum age assigned to the lowermost Tobas San Antonio unit is 3.3 ± 0.5 Ma. As deduced from the type of sediment, the fauna and the completeness of the fossils, the strata were deposited in a sandy tidal flat with significant wave activity (Johnson and Ledesma-Vázquez 2001).

El Refugio Formation.— The El Refugio Formation represents the youngest marine unit in the San José del Cabo Basin (Fletcher et al. 2003). The El Refugio Formation conformably overlies the Trinidad Formation; it is composed of ~ 380 m of light-gray colored medium to coarse arkosic sandstones as well as some fine-grained sandstone, shale, and limestone (Martínez-Gutiérrez and Sethi 1997). The unit is considered a regressive sequence based on its coarse grain size, ripple marks and fine cross laminations, abundant bioturbation and coarse shell deposits. A large number of specimens of *Solenastrea fairbanksi* Vaughan 1917 were collected from yellow middle-grained sandstone at Arroyo El Peyote near to Rancho Algodones (Fig. 6; Table 1) that is mixed with coquina and whole and fragmented marine mollusks. The age of the formation is not well constrained (Fletcher et al. 2003). Based on molluscan affinities (Smith 1991b.) and its conformable contact with the Trinidad Formation (Martínez-Gutiérrez and Sethi 1997; Pérez-López 2002), the unit is considered as early Pliocene. A more detailed analysis regarding the stratigraphic setting of the collecting localities is provided by Martínez-Gutiérrez and Sethi (1997), and Pérez-López (2002).

Pleistocene units.— A large number of Pleistocene reefs and flat-lying marine terraces of variable extension, from which coral taxa were collected, are distributed from Punta Chivato to Cabo Pulmo (Figs. 3–6; Table 1). Most of the Pleistocene reefs and marine terraces have been, to some extent, carefully described in the literature (Durham 1950; Squires 1959; Ashby et al. 1987; Ortlieb 1991; Sirkin et al. 1990; Libbey and Johnson 1997; Ransom 2000; Johnson and Ledesma-Vázquez 1999, 2001; Ledesma-Vázquez and Johnson 2001; Mayer et al. 2002; Muhs et al. 1994, 2002; DeDiego-Forbis et al. 2004; Johnson et al. 2007) and no further detail in stratigraphy or age is added.

Methods

Sampling.— Data were collected during four field expeditions to the Baja California peninsula in June-August 2002, January 2003, June-July 2003, and January 2005. For each coral-bearing unit under study, 1m^2 (1×1m) quadrats were systematically sampled. All quadrats were randomly placed in each coral-bearing stratigraphic horizon and all coral species within the quadrat were recorded. Specimen collection followed two approaches at each locality: (1) within each

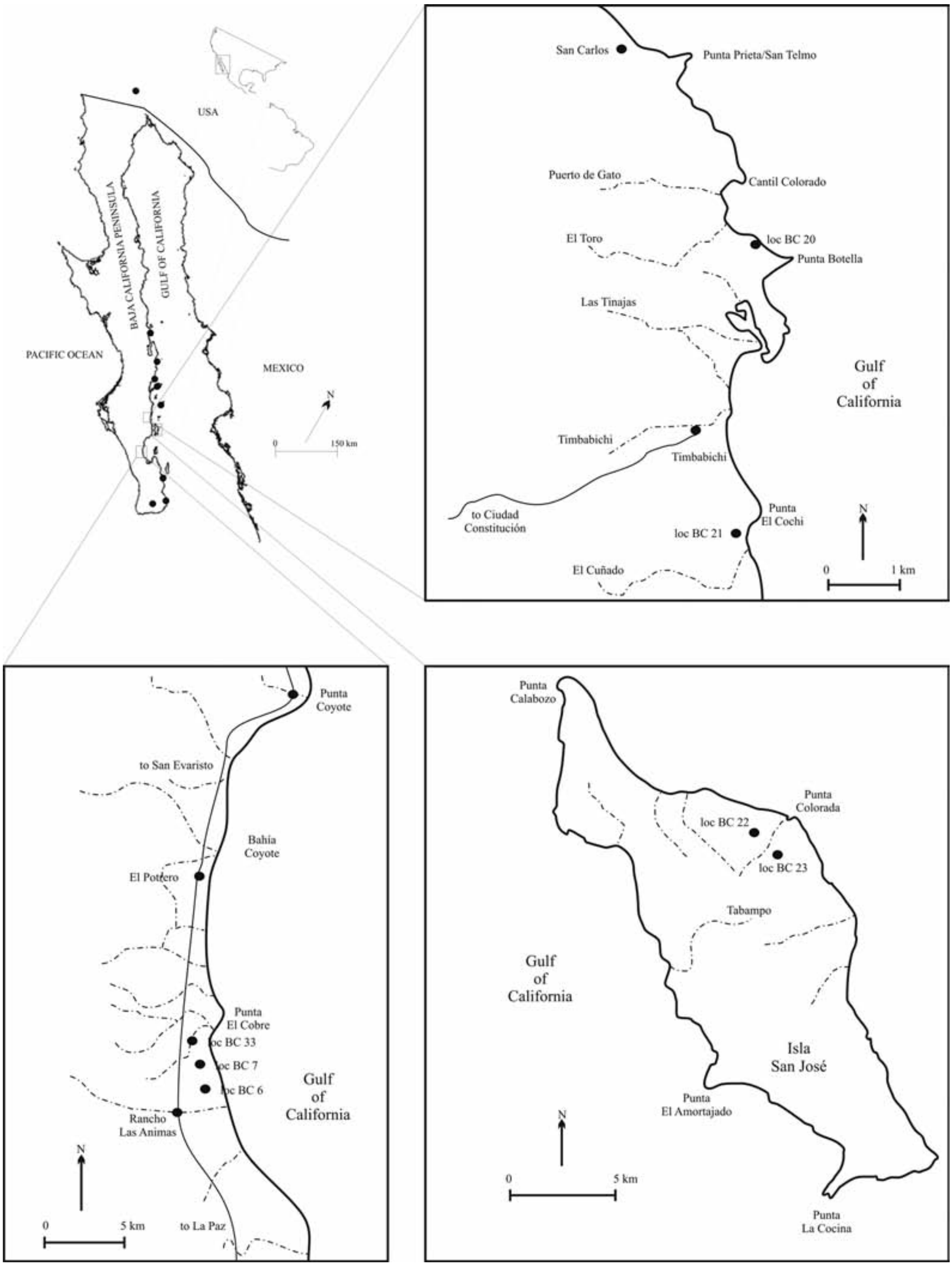

FIGURE 5. Collecting localities (●) at Timbabichi, Isla San José and Las Animas in the Gulf of California, northwestern México. Detailed information about each locality is listed in Table 1. Adapted from DeDiego-Forbis et al. (2004).

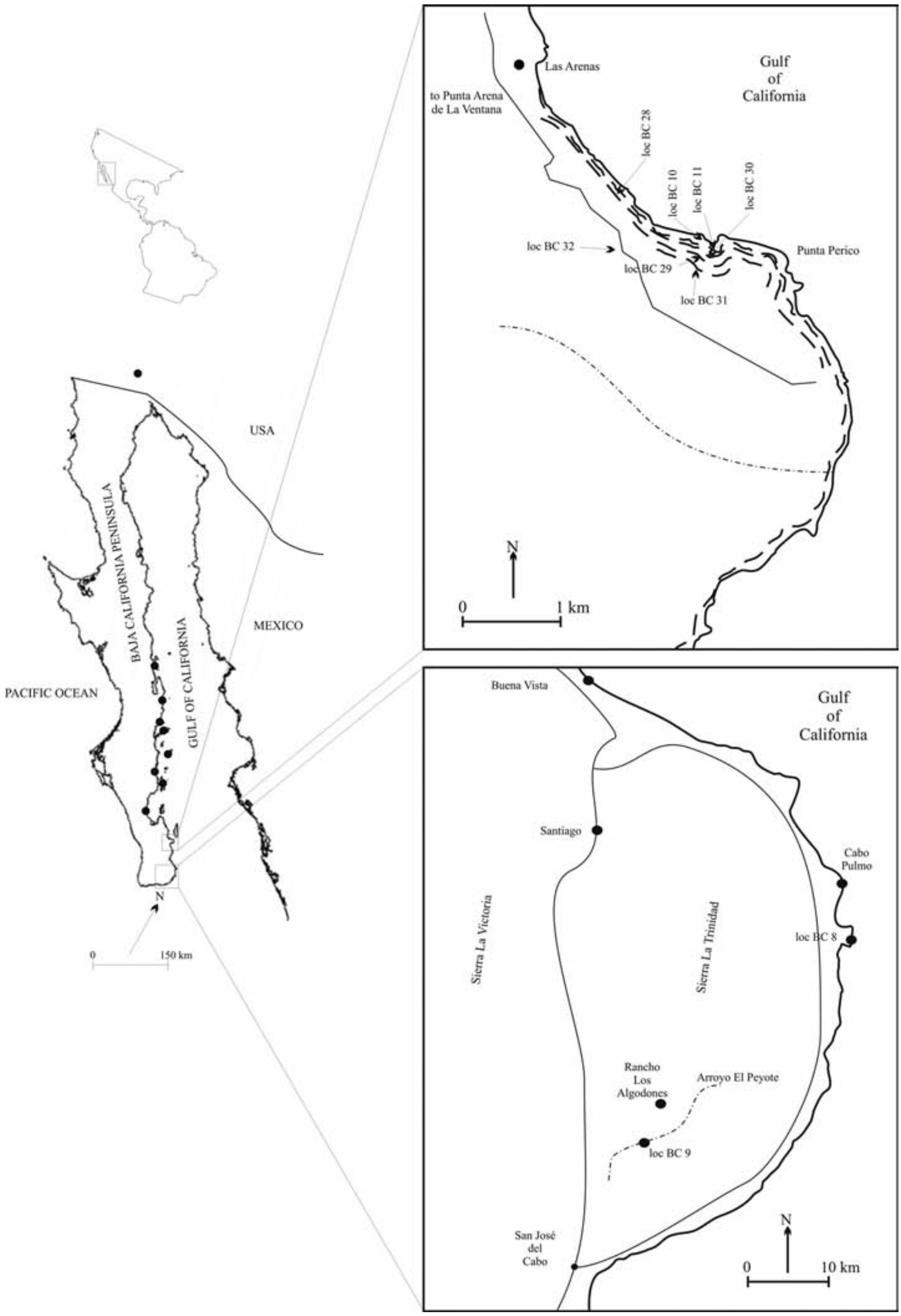

FIGURE 6. Collecting localities (•) at La Ventana and the San José del Cabo area in the Gulf of California, northwestern México. Detailed information about each locality is listed in Table 1. Adopted from Martínez-Gutiérrez and Sethi (1997).

quadrat, individual coral specimens were extracted from the face of the outcrop and (2) direct collection of unrecorded species during a thorough search of the locality.

Data analysis.— Species were identified by taking measurements directly on specimens and by analyzing the data following a rigorous morphometric protocol designed to detect distinct morphologic entities through geologic time (Budd and Coates 1992; López-Pérez et al. 2003). In general, specimens were identified and distinguished following a suite of geometric morphometric and traditional morphometric analysis, comparing fossil and modern specimens previously obtained from the Gulf of California (Durham 1950; Durham and Barnard 1952; Squires 1959), eastern Pacific (Reyes-Bonilla et al. 2005) and the Caribbean (Budd 1991; Budd et al. 1994; Budd and Johnson 1999). Species names were assigned to morphologic subgroups by quantitative comparison with holotypes of formally described species from the late Miocene to Recent Gulf of California, eastern Pacific, Indo-Pacific and Caribbean region. However, in cases where qualitative groups consist of fewer specimens, or when there is a lack of reliable calical structures and/or because structures are not available in large enough quantity to distinguish species using a statistical population approach, the subgroups were identified by qualitative comparison with previously described fossil and Recent species. Some identifications have been left in open nomenclature pending the formal taxonomic publication of the systematic work.

Results and Discussion

Twenty-three coral species were identified in Gulf of California fossil outcrops. Collections from the late Miocene Imperial Formation, the early Pliocene San Marcos Formation, the middle to late Pliocene Carmen Formation and the Pleistocene, Gulf of California, Mexico, have yielded four undescribed species *Siderastrea* sp., *cf. Placosmilia* sp., *Favia* sp. 1., and *Favia* sp. 2, and first time occurrences of the previously described *Pocillopora damicornis*, *P. verrucosa*, *P. meandrina*, *Gardineroseris planulata*, *Pavona clavus*, *Porites lobata*, *Diploria sarasotana* and *Dichocoenia eminens*.

Twelve out of 23 species are extant and 11 are extinct. The extant fauna is composed of *Pocillopora damicornis*, *Pocillopora capitata*, *Porites panamensis*, *Porites lobata* and *Pavona gigantea* Verrill 1869 considered among the major reef builder species in the Gulf of California, and Mexican and eastern Pacific communities (Reyes-Bonilla and López-Pérez 1998; Glynn and Ault 2000; Reyes-Bonilla et al. 2005); the restricted but common *Gardineroseris planulata*, *Psammocora stellata* (Verrill 1866), *Pavona clavus*, and the endemic *Porites sverdrupi* Durham 1947. The extinct fauna is composed of *Solenastrea fairbanksi*, *Porites carrizensis*, *Dichocoenia merriami*, *Diploria bowersi* (Vaughan 1917) and *Siderastrea mendenhalli* Vaughan 1917 previously reported from the Imperial Formation, Isla Tiburon, Punta Chivato and Isla María Madre (López-Pérez, 2005); the corals *Dichocoenia eminens* from the early Pliocene-early Pleistocene on the northern Caribbean, and *Diphoria sarasotana* from the early-late Pliocene, Tamiami Formation of Sarasota, Florida also in the northern Caribbean, and four species identified in the collections as *cf. Placosmilia* sp., *Siderastrea* sp., and two species of *Favia*, which will be described and named elsewhere.

Eight out of 23 species are temporally restricted to one location. Of these, four are restricted to early and middle to late Pliocene, one to middle Pleistocene and the rest to the late Pleistocene (Table 1). Nonetheless, restricted *Pocillopora meandrina*, and *Pocillopora verrucosa* also occur in the Recent of the Mexican Pacific, whereas *Diploria sarasotana* and *Dichocoenia eminens* also occur in the Pliocene of the Caribbean (*http://nmita.geology.uiowa.edu*). On the contrary, previously described *Porites carrizensis*, *Diploria bowersi*, *Solenastrea fairbanksi* and *Dichocoenia merriami* once considered restricted to the late Miocene Imperial Formation, Isla Tiburon and Isla Maria

Madre (Vaughan 1917; Jordan and Hertlein 1926; Hertlein and Emerson 1959; Simian and Johnson 1997; Gastil et al. 1999) are much more spatio-temporally distributed than previously thought (Table 1). For example, *P. carrizensis* was reported from the late Miocene-early Pliocene Imperial Formation of south-central California (Vaughan 1917); nonetheless it was recorded in the early Pliocene San Marcos Formation of Puerto de la Lancha, Punta Chivato and Ensenada El Muerto, middle Pliocene Carmen Formation of Isla Montserrat and late Pliocene Carmen Formation of Las Barracas (Table 1).

Particularly important is the presence of *Gardineroseris planulata* and *Porites lobata* on fossil outcrops of the Baja California peninsula area. *Gardineroseris planulata* contributed largely to reef formation during the middle Pleistocene at La Ventana; whereas *Porites lobata* reached Cabo Pulmo near the mouth of the Gulf during the late Pleistocene, nonetheless both species disappeared afterwards from the area. As a fossil, *Gardineroseris planulata* and *Porites lobata* occurred elsewhere in the late Miocene to Pleistocene of the Caribbean (Stemann 1991) and Indo-Pacific (Veron and Kelley 1988), but doubtfully in the eastern Pacific (Lopez-Perez 2005, but see Colgan 1990). Today, the closest positive record of *Gardineroseris planulata* is at the Bahías de Huatulco, Oaxaca in western Mexico (Leyte-Morales 1995) and in Central America (Cortés and Jiménez 2003) in the eastern Pacific, and from the Indian Ocean and Red Sea to the Central Pacific (Veron 2000); whereas *Porites lobata* is a widely distributed Indo-Pacific species recorded at Bahía de Banderas, Nayarit (Reyes-Bonilla et al. 1999) and Ixtapa-Zihuatanejo, Guerrero (Reyes-Bonilla et al. 2005) in western Mexico, and in Central America (Cortés and Jiménez 2003). In this regard, since both species were eliminated from the Baja California peninsula and no living representatives of the species have ever been reported from the area (Reyes-Bonilla et al. 2005), it can be considered as the first documented failed colonization of an Indo-Pacific species in the eastern Pacific.

Similarly, it is worth commenting on the occurrence of *Pocillopora capitata*. The species was first recorded in the Pleistocene of Isla Carmen, Isla Montserrat and Timbabichi (San Telmo Point) (Durham 1950), but the present work pushed back the record to the middle to upper Pliocene undifferentiated Carmen/Marquer Formation at Isla Carmen. The species was then spatially restricted to several Isla Coronados terraces (Table 1) but flourished all over the Gulf of California by the late Pleistocene. In the same way, the oldest record of *Porites panamensis* occurred in the Lower Pliocene San Marcos Formation at Ensenada El Muerto in the Punta Chivato area and at Puerto de La Lancha on Isla Carmen (Table 1), where relatively small but abundant massive and ramose colonies contributed to the community structure; afterwards, the species achieved a wide spatio-temporal distribution in the Gulf and formed monospecific reefs and constructions of variable combinations with relatively few species, nevertheless always dominated by *Porites panamensis* (Durham 1950, López-Pérez 2005, Johnson et al. 2007). From middle to late Pleistocene time, the relative importance of Indo-Pacific immigrants increased, but not until the Recent time were taxa other than *Porites panamensis* able to contribute in approximately the same amount to the reef construction in Gulf localities (Reyes-Bonilla and López-Pérez 1998; Reyes-Bonilla et al. 2002), and to overcome *Porites panamensis* elsewhere in Mexico and the eastern Pacific (Glynn and Wellington 1983, Glynn and Ault 2000, Reyes-Bonilla 2003; López-Pérez and Hernández-Ballesteros 2004).

The oldest occurrence of any Indo-Pacific species in the eastern Pacific corresponds to *Pocillopora eydouxi* Milne Edwards and Haime 1860 recorded by Palmer (1928) in late Pleistocene outcrops of Puerto Escondido, Oaxaca, Mexico, and *Psammocora stellata* and *Pocillopora elegans* Dana 1846 recorded by Durham (1950) also in late Pleistocene outcrops of Isla Coronados, Isla Carmena and Isla Montserrat. Nonetheless, recorded at La Ventana at the entrance of the Gulf of California (Fig. 1; Table 1) in outcrops dated by Sirkin et al. (1990) older than 0.3 million years, and at Isla Coronados in outcrops dated by Johnson et al. (2007) as having 121,000 years, *Pavona clavus* deserves being mentioned as the first documented Indo-Pacific immigrant to mainland America and the first fossil record of the species in the eastern Pacific. Outside the Gulf of California, the species occurs in the Miocene of Nias, Plio-Pleistocene of Ceram and in the Pleistocene of Java, Sumatra, Nias and New Caledonia in Southeast Asia (Veron and Kelley 1988). In México, it occurs in the Recent of Jalisco, Colima, Oaxaca (Reyes-Bonilla and López-Pérez 1998) and Islas Revillagigedo (Ketchum and Reyes-Bonilla 2001). It also occurs in Costa Rica, Panamá, Colombia, Ecuador and Clipperton Atoll (Reyes-Bonilla 2002). Outside of the eastern Pacific, it ranges from the Red Sea to the Central Pacific (Veron 2000). In addition, data suggests that after the arrival of *P. clavus* at La Ventana some time earlier during the Pleistocene, transpacific colonization became a common and relatively successful event.

Finally, in the future the odds that additional scleractinian fossil species will be described or discovered in the Gulf of California and/or eastern Pacific are high. Considering that 75% of the 16 hermatypic species in the Gulf of California, and just 27% of 44 eastern Pacific species (Reyes-Bonilla 2002) have fossil records, the probability to add fossil species to those presented here is high. Analysis using randomly resampled cumulative species curves performed by López-Pérez and Budd (in press) demonstrated that that species did not reach saturation in the Baja California Peninsula area, suggesting that additional collecting, especially within Upper Miocene and Lower Pliocene strata, is likely to result in the discovery of new taxa, especially after the inspection of new exposures from a wide range of environmental settings.

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